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RESTORATION OF VITALITY THROUGH CONJUGATION

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The physiological effect of conjugation, or fertilization, has been interpreted, in the main, along two lines of theory. One of these may be indicated by Bütschli's term *Verjüngung*, and by Maupas's corresponding one *rajeunissement*, terms indicating that the primary effect of conjugation is to restore vital activities to an optimum. The other theory, first fully elaborated by Weismann, assumes that the union of germ plasms (amphimixis), brought about by conjugation, is a source of variations.

These theories are not reciprocally exclusive, and it is possible that both are correct, although neither has been conclusively established.

Bütschli interpreted conjugation in the protozoa, as a means whereby waning vitality is restored to full metabolic activity. The problem thus suggested, involves three fundamental questions: (1) Does the protoplasm of a single individual protozoon and its progeny by division, undergo a progressive waning of vital activities leading to 'old age,' degeneration, and, finally, to natural death? (2) Does conjugation actually restore such weakening protoplasm to a condition of full metabolic activity? (3) If conjugation accomplishes this, what is the explanation of the result?

The first of these three questions was answered in the affirmative by the experiments of Maupas and of numerous subsequent investigators. The second has never been answered conclusively, although strong experimental evidence has accumulated in support of the affirmative. The third question, obviously, is dependent on the second and will be disregarded here.

In the present preliminary paper, I submit the results of experiments made during the last year and a half, which offer a positive answer to the second of these three questions, affording proof that conjugation, in the ciliated protozoon Uroleptus mobilis, actually restores waning vitality to full metabolic vigor. These results are based on the records of the progeny of a

single individual cell, which have been maintained under identical conditions and fed daily with the same standardized culture medium.

The usual method of isolating single individuals each day in fresh culture medium, has been used throughout; five "lines" of individuals of the same ancestry forming a 'series.' Being isolated each day, conjugation never occurs in the culture dishes.

After the daily isolations, the residual individuals are either thrown away, or are put together in larger culture dishes containing fresh culture medium. Here they are kept for a period of two weeks without renewal of the culture medium. At first there is an abundance of food and the organisms multiply by fission until three or four thousand are present. Later, the food becomes exhausted, and, as is well known in some other cases, the transition from rich feeding to starvation induces conjugation, provided the organisms are sexually mature. This procedure constitutes a "conjugation test" which is carried out at weekly intervals.

The number of divisions per day in each of the five lines of a series is recorded; also the sum of the daily divisions, giving a total number of generations to date in each line. The daily records of all lines of a series may then be averaged for successive periods of ten days each, such averages giving a convenient and accurate representation of the relative metabolic activity at different periods of the life cycle.

From time to time, individuals that have undergone conjugation in the weekly conjugation tests, may be isolated to form the beginnings of filial series which are maintained in isolation cultures exactly as in the original series. From the methods employed in these tests, it is evident that such conjugations take place between rather closely-related individuals which are of the same age. The protoplasm affected by such conjugation, also, has had the same history and the same daily treatment throughout, as that maintained in the isolation cultures. After conjugation, a filial series is continued in isolation cultures, transferred daily to the same medium as that used for the parent series, and parallel records are kept in the same way. A filial series, therefore, represents the same original protoplasm as that represented by isolation cultures of the parent series. Any difference in the same calendar periods between the records of the parent series, and those of the filial series, must, therefore, be attributed to the conjugation that has taken place between the closely-related cells of the parent series.

An ideal culture medium for Uroleptus, was found to be an infusion made by boiling a small quantity of flour and a small quantity of fine-cut hay in spring water. This infusion should be used only after twenty-four hours exposure to the air. After the first fifty days of experimenting, this culture medium, made fresh each day, has been used without any alterations.

I have found that the process of 'endomixis' or asexual reorganization with restoration of vitality, occurs in Uroleptus mobilis while encysted. Such encysted stages persist for long periods, and I find that the organisms cannot

be recovered from the cysts until they have been dried for some weeks. The process of reorganization, therefore, cannot escape observation, and it has never occurred in the isolation cultures. The uniformity of results in all of the series outlined below, is sufficient evidence that no other method of asexual reorganization, or parthenogenesis, has occurred in any isolation culture.

A single ex-conjugant from a pair of 'wild' conjugating individuals was isolated on Nov. 24, 1917. It formed the parental series, or, as I shall call it, the '*A* series' and I would explicitly state again, that all results described here, have been obtained with lineal descendants, by division, of this one ancestral cell, and without change of the culture medium.* Five lines were established at the third division and the relative vitality, at successive ten-day periods, is shown in column 1 of table 1. The series ran through 313 generations by division and died out after a long period of progressively reduced vitality, on September 18, 1918.

Conjugation tests were made every week and gave constant epidemics of pairing after the first six weeks. A single pair of conjugating individuals was isolated on four different occasions. In each case the pair was watched until the two individuals had separated. One of the ex-conjugants on each occasion, was then isolated as the starting individual of a filial series. The first of these ex-conjugants formed the filial C series and came from a pair which were in the 78th generation of the parent A series, on February 4, 1918. The second, formed the filial D series which came from a pair of the A series conjugating on March 8, 1918, in the 137th generation. The third, formed the filial H series, which came from a pair conjugating on May 17, 1918, in the 237th generation of the parent A series. The fourth formed the filial J series which came from a pair conjugating on August 12, 1918, in the 311th generation of the parent A series. The parent A series died from exhaustion in the 313th generation, hence these four filial series were taken off at different periods of waning vitality of the parent protoplasm. Each was maintained in five lines and treated exactly like the parent isolation series. Their histories, in successive ten-day periods, are shown in columns 2, 3, 4 and 5.

The history of the C series was similar to that of the parent A series. After a long period of progressively reduced vitality it died on December 31, 1918, in the 348th generation. The D series outlived the parent series but did not live as long, dying after 230 days in the 271st generation. The H series is still alive and is now (January 8, 1919) in the 277th generation. The J series was taken from the parent A series when vitality of the latter was very low, each individual of the parent series dividing only 2.2 times in ten days. The effect of conjugation, as shown by the J series was to increase the division rate to 17.2 times in ten days, while, for the same calendar period, the parent series was dividing at the rate of two-tenths of one division in ten days. The J series is still dividing actively in the 236th generation.

* At the present time (March 15) descendants are still living with unimpaired vigor.

TABLE 1

AVERAGE DIVISION RATE PER INDIVIDUAL, IN TEN-DAY PERIODS

10-DAY PERIODS	A SERIES	C SERIES	D SERIES	H SERIES	J SERIES	F SERIES	I SERIES	L SERIES	PARENTAGE
1	9.8								C series from A78th generation
2	6.6								D series from A137th generation
3	4.8								H series from A237th generation
4	5.4								J series from A311th generation
5	7.8								F series from C86th generation
6	21.0								I series from F143d generation
7	18.6								L series from I199th generation
8	20.8	18.6							
9	18.0	18.8							
10	12.6	16.2							
11	13.2	16.8	16.0						
12	14.8	17.2	18.2						
13	14.6	15.6	16.0			13.4			
14	13.2	14.2	17.0			13.8			
15	15.0	16.4	17.6			16.4			
16	13.6	15.6	18.4			19.8			
17	17.0	17.4	19.0			20.2			
18	12.8	18.0	20.0	19.6		19.6			
19	7.4	13.4	15.2	16.8		15.8			
20	11.0	14.4	16.6	17.8		16.8			
21	7.0	12.8	14.4	15.8		14.0			
22	9.0	10.4	13.4	14.8		12.8			
23	7.6	11.4	14.6	19.1		14.2	18.4		
24	11.2	17.6	18.4	21.4		19.8	22.6		
25	4.8	10.6	12.6	16.4		13.8	19.4		
26	2.2	9.0	10.4	18.0		15.2	11.8		
27	0.2	9.8	9.4	15.6	17.2	12.0	15.0		
28	0.6	8.6	3.4	15.6	16.6	11.8	15.8		
29	0.2	7.6	1.4	15.4	18.6	10.8	14.8		
30	0.0	6.0	0.8	17.8	17.4	12.0	17.6		
31	*Dead*	6.8	0.4	17.8	20.4	14.6	18.0		
32		4.8	0.2	11.0	17.2	9.8	11.6		
33		2.4	0.0	15.4	15.8	9.6	16.4		
34		0.6	0.0	12.6	17.2	12.0	17.4		
35		0.0	*Dead*	7.4	14.6	8.0	14.0	16.0	
36		0.4		2.4	12.4	5.8	12.8	13.2	
37		0.4		1.6	14.4	3.8	13.8	16.2	
38		0.0		1.6	20.6	2.8	20.8	23.2	
39		0.0		0.4	17.0	0.0	15.8	18.6	
40		*Dead*		1.2	12.6	*Dead*	13.0	16.0	

The F series was started with an ex-conjugant of the C series in the 86th generation, and died December 21 in the 317th generation, ten days earlier than the parent series. The I series was taken from the F series in the 143d generation and is still living actively in the 305th generation. The L series came from this I series in the 199th generation and is actively dividing in the 118th generation. An N series (not included in the table) has recently been started from the J series in the 188th generation.

While table 1 by itself, shows clearly enough that conjugation restores vitality to an optimum, the results may be shown still more strikingly by a comparison of longer periods of time whereby minor fluctuations are less conspicuous. I find from the records of the conjugation tests of all series, that conjugation does not begin to take place until from fifty to seventy days from the start of a series. I have chosen the period of the first sixty days, therefore, as representing the period of sexual immaturity. The records show, furthermore, that this is also the period of optimum metabolic activity.

Comparing the mean division rate of a filial series in this first sixty day period, with the division rate of the parent series for the same calendar sixty days, shows the extent, in division activity, to which conjugation has restored vitality to the parent protoplasm. Thus, during the first sixty days of the C series, the five lines had a mean daily division rate of 8.6333, or each individual averaged 1.726 divisions per day, or in ten days, 17.2666 divisions. In the same sixty days, the parent A series, starting at the 78th generation, had a mean division rate of 7.8666 daily, each individual averaging 15.7333 divisions in ten days. The difference, 1.53, indicates the average increase, in number of divisions in a ten-day period, of each individual of the C series, over each individual of the parent A series. In this case the filial generation was taken from the parent when vitality of the latter was near its optimum, and a small discrepancy between parent and offspring is to be expected. With increasing age of the parent, and with corresponding reduction in vitality of its protoplasm, one might reasonably expect that conjugation between two such weakened individuals, would result in a filial generation in which the discrepancy between parent and offspring would remain practically the same as above. The results, however, do not support this expectation; on the contrary, the discrepancy increases with age of the parent protoplasm, as shown in table 2.

It is evident, from the foregoing, that conjugation results in the complete restoration of vitality regardless of the age or the weakened condition of the parent protoplasm, although both parental and filial series are fed at the same times on exactly the same culture medium. This is particularly striking in the case of the J series.

Table 2 also shows that all filial series return to a certain optimum of metabolic vigor as a result of conjugation, a vigor represented by from 17.1 to 17.9 divisions per individual in ten days. From this optimum there is a gradual loss of vitality which is common to all series and which finally leads to death from old age. This is clearly shown in table 3.

TABLE 2

COMPARISON OF DIVISION RATES OF PARENT AND OFFSPRING DURING FIRST SIXTY DAYS OF LATTER

	C FROM A SERIES	SERIES	D FROM A SERIES	SERIES	B FROM A SERIES	SERIES	J FROM A SERIES	SERIES	F FROM C SERIES	SERIES	I FROM F SERIES	SERIES
Dates	2/7 — 4/8		3/8 — 5/7		5/22 — 7/21		8/16 — 10/15		3/28 — 5/27		7/7 — 9/5	
Parent's age	78 generations		137 generations		237 generations		311 generations		86 generations		143 generations	
Mean division rate per day, all 5 lines	8.6333	7.8667	8.5833	7.0666	8.6666	6.2666	8.9666	0.125	8.6000	8.1000	8.5833	6.5666
Average division rate per individual per ten days of period.	17.2666	15.7334	17.1666	14.1333	17.3332	12.5332	17.9332	0.2500	17.2000	16.2000	17.1666	13.1332
Increase per individual per ten days of period.	1.5332		3.0333		4.8000		17.6832		1.0000		4.0334	

TABLE 3

DIVISION RATES IN SUCCESSIVE SIXTY-DAY PERIODS, ALL SERIES

SERIES AND ORIGIN	FIRST 60 DAYS			SECOND 60 DAYS			THIRD 60 DAYS			FOURTH 60 DAYS			FIFTH 60 DAYS			SIXTH 60 DAYS
	Mean division rate per day, all 5 lines	Division rate per individual per 10 days of period	Date	Mean division rate per day, all 5 lines	Division rate per individual per 10 days of period	Date	Mean division rate per day, all 5 lines	Division rate per individual per 10 days of period	Date	Mean division rate per day, all 5 lines	Division rate per individual per 10 days of period	Date	Mean division rate per day, all 5 lines	Division rate per individual per 10 days of period	Date	
A "Wild" exconjugant 11/15/'17	*	*	11/28 to 1/27	8.183 ±0.1985	16.366	1/28 to 3/29	7.183 ±0.1645	14.366	3/29 to 5/28	4.450 ±0.1822	8.900	5/28 to 7/27	0.6667 ±0.1300	1.333	7/27 to 9/25	Dead 9/18
C From A78 2/4/'18	8.6333 ±0.2185	17.266	2/ 9 to 4/ 8	7.9167 ±0.1809	15.833	4/ 9 to 6/ 8	6.4166 ±0.1945	12.833	6/ 8 to 8/ 5	3.9834 ±0.1760	7.966	8/ 5 to 10/ 4	0.7166 ±0.0593	1.433	10/ 4 to 12/ 4	Dead 12/31
D From A137 3/8/'18	8.5833 ±0.1349	17.166	3/ 8 to 5/ 7	8.1666 ±0.2475	16.333	5/ 8 to 7/ 7	5.7834 ±0.2374	11.566	7/ 7 to 9/ 5	0.3500 ±0.0737 (40 days	0.700 only)	9/ 5 to 10/15	Dead 10/15			
H From A237 5/17/'18	8.6666 ±0.1892	17.333	5/22 to 7/21	8.5333 ±0.2165	17.066	7/16 to 9/14	7.0000 ±0.2495	14.000	9/15 to 11/14	Not completed.						
J From A311 8/12/'18	8.9666 ±0.2252	17.933	8/16 to 10/15	7.9167 ±0.1956	15.833	10/15 to 12/14	Not completed.									
F From C86 3/25/'18	8.6000 ±0.2320	17.200	3/28 to 5/27	7.7834 ±0.2313	15.566	5/27 to 7/26	6.3333 ±0.1690	12.666	7/26 to 9/24	4.8833 ±0.2100	9.766	9/24 to 11/23	Dead 12/21			
I From F143 7/1/'18	8.5833 ±0.2468	17.166	7/ 7 to 9/ 5	7.9834 ±0.2320	15.966	9/ 5 to 11/ 4	7.5166 ±0.2256	15.0332	11/ 4 to 1/ 3	Not completed.						
L From I199 11/2/'18	8.7000 ±0.2986	17.400	11/ 4 to 1/ 3	Not completed.												

* Culture medium not established until 55th day.

From this table it is evident that all series follow the same general history, and that, at corresponding periods of the life cycle, all have about the same vigor, although the actual dates may range through all twelve months of the year.

The experiments thus show not only that waning vitality leading to old age and natural death is manifested by Uroleptus mobilis, but also, that conjugation between two individuals at any stage of waning vitality, leads to a complete restoration of vitality.

FALKLANDIA

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Falklandia is a name herewith applied to a continental land which, during the Devonian period in the occidental parts of the Southern Hemisphere, preceded Gondwana-Land and Antarctis. The history of Gondwana-Land is well established (Neumayr, Suess); its supposed earliest outlines have been approximately determined by the study of its land flora (D. White). The conception of Gondwana-Land is that of a great east-west southern continent which escaped the turmoil of world-wide postcarboniferous deformations and which continued its existence as a continental asylum for land and stream life till late in the Mesozoic time (Cretaceous) when incursions of the sea began which led to its breakdown and demolition in the Tertiary. Eastern Brazil into Sao Paulo, southern Argentine and the north half of the Falkland Islands constitute its western fragments; South Africa, the lost Lemuria (from Madagascar to Ceylon), India and Australia indicate its western extent. Those who have been responsible for the determination of this continent and especially Suess, who has discussed it in much detail, have not recorded its existence prior to the Carboniferous. Antarctis likewise, another Southern 'asylum,' defined on the basis of its terrestrial life and never accurately delimited by its proponents as to the date of its origin, gives proof of like beginning of stabilization and perhaps also of length of endurance. The fossil woods discovered in the Beacon sandstone of South Victoria-Land by James Eights ninety years ago, and the fossils brought home in recent years by Andersson, Nordenskiold, Amundsen, Shackelton and the men of Scott, tend to indicate that it was coexistent in time with Gondwana-Land.

Asylums, thought Suess, were to be defined by continuity in the succession of terrestrial life; it must be added, however, that security of such determinations can be given by the character of the life of the sea which washed the shores of such asylums. Gondwana-Land and Antarctis had a parallel existence in time, though a distinct one. Osborn's observations indicate the

breakdown of Antarctis in the Tertiary. Both Gondwana-Land and Antarctis had a far longer duration than any of the continents of today.

In the period immediately preceding the isolation of these continental masses they were united at the west; that is, in the occidental South Atlantic, the south polar land extended continuously into the land regions of the Gondwana Continent. This we know from the determinations of the Devonian strand lines in southern South America, the Falkland Islands and South Africa.

The Devonian of these latitudes is a unit both in life and in sedimentation. In this regard it is wholly unlike the Devonian of Eria, the east-west continent of the North, and it is a conclusion that is irrefragable on the basis of the intimate and refined analysis that such determinations require and have received. The haphazard observer may be blind to these radical distinctions, especially when basing interpretations upon a knowledge of the strand faunas of Eria. The known extent of these Southern Devonian shore faunas, as pointed out by the writer (Fosseis Devonianos do Parana; Monographias, Vol. I, Servico Geol. e Mineral do Brazil, 1913), indicates the union of the Gondwana and Antarctis continents throughout the Devonian. The extent of this Devonian land bridge across the Atlantic is clearly shown by the unity of shore faunas in South Africa, Sao Paulo, Argentine and Bolivia, and the indication is of a land composed of Paleozoic strata of still earlier date. This is Falklandia, the parent land asylum out of which, in Postcarboniferous time, western Gondwana and Antarctis were carved. The name is appropriately taken, for on the Falkland Islands the Devonian marine strata border the Gangamopteris (Glossopteris) beds of Gondwana-Land.

Other names which have been suggested for these pre-Gondwana austral lands have been founded on inadequate evidence. The "South Atlantic Island" of Frech indicated a Devonian land which had no connection with South Africa; Katzer imagined a north-south Devonian Atlantis running along the axis of the ocean, and Schwarz drew, with somewhat freer hand, his "Flabellites Land," as an undivided land mass along the Atlantic axis reaching from the north, and at the south spreading west and east to join Frech's "South Atlantic Island."

ON THE REAL FOLDS OF ABELIAN VARIETIES

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1. In this note we propose to find the number of real folds that an abelian variety of rank one may have and to establish some simple properties regarding their connectivity.

An abelian variety of genus p, V_p, belonging to an S_n, $(n > p)$, is defined by equations

$$x_j = f(u_1, u_2, \ldots u_n), \ (j = 1, 2, \ldots n) \qquad (1)$$

where the (f)'s are $2p$-ply periodic meromorphic functions of the (u)'s, the periods forming a matrix Ω of a type called, after Scorza, a Riemann matrix. The rank of V_p is the number of distinct systems of values of the (u)'s, modulo Ω, corresponding to an arbitrary point of V_p. It is easy to show that to any Ω corresponds a V_p of rank one. Suppose indeed the (f)'s so chosen that any other periodic meromorphic function φ belonging to Ω be a rational function of them. If V_p were of rank > 1 then to every set of values $(u_1, u_2, \ldots u_p)$, would correspond another $(u_1', u_2', \ldots u_p')$, distinct modulo Ω, such that $\varphi(u) = \varphi(u')$ whatever φ. Choosing p such functions with non zero jacobian we find that the (u')'s are functions of the (u)'s. But $\varphi(u_1' - \alpha_1, \ldots u_p' - \alpha_p) = \varphi(u_1 - \alpha_1, \ldots u_p - \alpha_p)$ whatever the constants α, since the function at the right is of same type as φ. Hence at once $du_k' = du_k$, $u_k' - u_k = \beta_k$. The (β)'s are constants which obviously form a set of periods of the (f)'s, and therefore V_p is effectively of rank one.—All abelian varieties of rank one belonging to Ω are birationally equivalent.

2. Denoting by $\bar{m}$ the complex conjugate of any number m, a real variety of S_m is defined by the condition that when it contains one of the points, said to be conjugate, (x), $(\bar{x})$, it contains the other. Let then Ω be a Riemann matrix with a corresponding real V_p of rank one. Any simple integral of the first kind of V_p is of the form $u = \int \Sigma R_j \, dx_j$, where the (R)'s are rational in the (x)'s. Replacing in them all coefficients by their conjugates we obtain a new integral of the first kind of V_p, say (u), and u is a linear combination of the two integrals $u + (u), -i(u - (u))$, which are of real form. Hence V_p possess p independent integrals of real form, $u_1, u_2, \ldots u_p$. If V_p has a real point and we take it for lower limit of integration, our integrals will assume conjugate values at conjugate points of V_p.

Let now γ be any linear cycle of V_p and $\bar{\gamma}$ its transformed by T, transformation of the variety permuting each point with its conjugate. T transforms $\gamma + \bar{\gamma}$ into itself and $\gamma - \bar{\gamma}$ into its opposite. As $2\gamma, = (\gamma + \bar{\gamma}) + (\gamma - \bar{\gamma})$, the double of any cycle is the sum of two others transformed by T the one into itself and the other into its opposite. The periods of u_k with respect to cycles of the first type are real, and with respect to those of the other type they are pure complex. If q is the number of cycles of one type $2p - q$ is that of the cycles of the other type. As the real and complex parts of the periods of p independent integrals of the first kind with respect to $2p$ independent cycles form a non zero determinant, we must have $q = 2p - q$, or $q = p$. Finally we may single out $2p$ cycles $\gamma_1, \gamma_2, \ldots \gamma_{2p}$, such that $T.\gamma_k = \gamma_k$, $T.\gamma_{p+k} = -\gamma_{p+k}$, $h \leqq p$ while the cycles $m_1\gamma_1 + m_2\gamma_2 + \ldots + m_{2p}\gamma_{2p}$, ($m_k$ integer), include the double of any cycle of V_p. The corresponding period matrix for the (u)'s is of the type

$$\| \omega_{h,1}, \omega_{h,2}, \ldots \omega_{h,p}; i\omega_{h,p+1}, i\omega_{h,p+2}, \ldots i\omega_{h,2p} \|, \quad (h = 1, 2, \ldots 2p) \tag{2}$$

the (ω)'s being real.

Remark.—In all this V_p could be replaced by any real irreducible algebraic variety of irregularity p.

3. Conversely if to Ω corresponds a V_p of rank one with $2p$ linear cycles $\gamma_1, \gamma_2, \ldots \gamma_{2p}$, such that the cycles $m_1\gamma_1 + m_2\gamma_2 + \ldots + m_{2p}\gamma_{2p}$ include the double of any other, while p independent integrals of the first kind $u_1, u_2, \ldots u_p$, have with respect to them a period matrix of type (2), V_p is birationally equivalent to a real abelian variety. Indeed as a consequence of the assumptions made, if the equations (1) represent V_p, and if $(\omega_1, \omega_2, \ldots \omega_p)$ are a set of periods of the (f)'s so are $(\bar{\omega}_1, \bar{\omega}_2, \ldots \bar{\omega}_p)$. Moreover the (f)'s are real meromorphic functions of the (u)'s and of a finite number of constants. If we replace these constants by their conjugates we obtain new functions $f(u_1, u_2, \ldots u_p)$ with the same periods as the (f)'s the equations

$$x_j' = f_j + \bar{f}_j, \; x_j'' = -i(f_j - \bar{f}_j), \; (j = 1, 2, \ldots n)$$

represent in an S_{2n} a real abelian variety birationally equivalent to V_p. This real abelian variety has ∞^p real points.

4. Assuming then V_p real with real folds, to determine their number we remark that at two conjuguate points the integrals u_h of No. 2 take conjuguate values $u_h' + iu_h''$, $u_h' - iu_h''$, modulo Ω. At the real folds the (u)'s are given by $u_h' + \frac{i}{2}\sum_1^p{}_\mu r_\mu \omega_{h,p+\mu}$, ($u_h'$ arbitrary, $r_\mu = 0$ or 1; $h = 1, 2, \ldots p$). There are in general $p - s$ periods of this type such that no linear combination of them with integral coefficients is of the form

$$\sum_1^p{}_\mu (m_\mu \omega_{h,\mu} + im'_\mu \omega_{h,p+\mu}), \; (h = 1, 2, \ldots p).$$

Hence $p - s$ of the integers r can be made equal to zero. Taking the others equal to zero or one yields 2^s distinct real folds.—That there are varieties having that number of real folds whatever $s \leqq p$ is shown by the canonical matrix

$$\left\| \begin{array}{l} 1, 0 \ldots 0, \; a_{11}, \; a_{12}, \ldots a_{1p} \\ 0, 1 \ldots 0, \; a_{21}, \; a_{22}, \ldots a_{2p} \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ 0, 0 \ldots 1, a_{p1}, \ldots\ldots a_{pp} \end{array} \right\|$$

($a_{\mu\nu} = a_{\nu\mu} = \frac{1}{2} m_{\mu\nu} + i a''_{\mu\nu}$; $m_{\mu\nu}$ integers forming a matrix of rank s modulo 2; the quadratic form $\Sigma a''_{\mu\nu} x_\mu x_\nu$ is definite, positive.)

Hence a real abelian variety can have any number of real folds given by 2^s, $0 \leqq s \leqq p$.

5. Any real fold of the variety can be transformed into any other by a birational transformation belonging to the continuous group $(u_h, u_h + c_h)$. Hence

the real folds form equivalent p dimensional cycles, and the $q \leqq p$ dimensional ones which one of the folds contains are equivalent to some cycle, on any other. Moreover the real folds form homeomorphic manifolds. One of them is defined by the relations $u_h = \sum_1^p t_\mu \omega_{h\mu}$, where the (t)'s are real parameters varying from zero to one. It follows that any one of the folds corresponds point by point to the interior of a p-dimensional cube in the same manner as the points of a ring to those within a square. From this follows readily that the real folds are two sided manifolds of j-th index of connection equal to (p_j); this being also the number of independent real cycles of V_p. We may remark finally that each real fold is transformed into itself by the two sets of birational transformations, $(u_h, u_h + c_h)$, $(u_h, -u_h + c_h)$, where the (c)'s are real constants.

6. It is of interest to consider the types of real Jacobi varieties.—The Jacobi variety V_p of a curve of genus p, C_p, is an abelian variety of rank one belonging to the period matrix of p independent integrals of the first kind of C_p. Let C_p be real and its integrals of the first kind $v_1, v_2 \ldots v_p$ real in form with a real point M_0 for lower limit of integration. We assume that C_p has $q > 0$ real branches. We may then take for V_p a representation (1), the (f)'s being real functions of the variables u, now defined by $u_h = \sum_1^p \int_{M_0}^{M_j} dv_h$, the points $M_1, M_2, \ldots M_p$, being alone variable on C_p. In order that the point which corresponds to them on V_p be real it is necessary and sufficient that the set of the (M)'s coincide with that of their conjuguates,—a corollary of the fact that when a point of V_p moves on a real fold the increments of the (u)'s are real.

Let $B_1, B_2, \ldots B_q$, be the real branches of C_p. If we constrain α_1 of the (M)'s to be on B_1, α_2 on $B_2, \ldots \alpha_q$ on B_q, the corresponding point of V_p will be on a definite real fold F_1 of the variety, provided of course that $p - \Sigma \alpha_i$ be $\geqq 0$ and even. Assume one of the (α)'s, for example α_1, to be greater than one. I say that the fold F_2 corresponding to the integers $\alpha_1 - 2, \alpha_2, \ldots \alpha_q$, coincides with F_1. Indeed a ready corollary from our previous discussion is that two distinct real folds of an abelian variety have no common points, while F_1 and F_2 intersect along the $p - 1$ dimensional manifold obtained when α_1 of the (M)'s of which two coincide are on B_1, the $p - \alpha_1$ remaining being disposed as previously. Hence if $q \leqq p + 1$, V_p has as many real folds as there are independent solutions of the congruence $\Sigma \alpha_i - p \equiv 0$, modulo 2, that is 2^{q-1}. If $q > p + 1$, V_p would have more than 2^p real folds. As this is impossible, $q \leqq p + 1$ and we have here a new proof of Harnack's theorem that a curve of genus p has at most $p + 1$ real branches.

We see then that a Jacobi variety can have any number of real folds given by 2^s, s being an integer at most equal to the genus p.

COVARIANTS OF BINARY MODULAR GROUPS

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To transform the general case of a binary quantic

$$f_m = (a_0, a_1, \ldots, a_m)(x_1, x_2)^m,$$

by substituting for its variables

$$x_1 = \lambda_1 x_1' + \mu_1 x_2', \; x_2 = \lambda_2 x_1' + \mu_2 x_2',$$

where the coefficients of the transformation are least positive residues of a prime number p, is to generate an infinitude of binary forms associated with f_m, which are invariants of the linear modular group G of order $(p^2 - p) \times (p^2 - 1)$, on the variables x_1, x_2.

Much difficulty has been encountered by those who have investigated these invariants, both as to methods of generating complete systems and as to proofs of their finiteness. This paper is in the form of a summary of the present writer's research on this problem. It contains an outline of a method of construction of the formal modular covariants which has a measure of generality, —and which has proved to be definitive,—at least for particular moduli. Secondly we give, in explicit form, the finite modular systems of the cubic (mod 2) and of the quadratic (mod 3). Phases of the formal modular theory not mentioned in this paper are treated in articles by the present writer, referred to at the end of this paper, and in Dickson's Madison Colloquium lectures.

1. Modular convolution.—If $S(a_0, a_1, \ldots)$ is any modular seminvariant of f_m which satisfies a certain pair of conditions,[5e] and $a_0', a_1', \ldots$ are the coefficients of the transformed of f_m by means of

$$x_1 = x_1 + tx_2', \; x_2 = x_2'; \; (t \text{ any residue mod } p),$$

then, S' being the conjugate to S under the substitution $(a_0a_2)(a_1)$,

$$S'(a_0', a_1', \ldots) \equiv S(a_0, \ldots)t^{p-1} + S_1t^{p-2} + \ldots + S_{p-1} \pmod p, \quad (1)$$

written with homogeneous variables x_1, x_2, instead of t, is a formal covariant modulo p. When this principle is applied in the case of the seminvariant leading coefficient of the covariant K_ν:

$$K_\nu = C_0x_1^\nu + C_1x_1^{\nu-1}x_2 + \ldots + C_\nu x_2^\nu,$$

where ν is a number of the form

$$\nu = (sp - \nu')(p - 1) = \sigma(p - 1),$$

there results a covariant[8]

$$[K_\nu] = [C_0 + (K_\nu)]\, x_1^{p-1} + \sum_{r=0}^{p-2} \sum_{s=0}^{\sigma-1} C_{\nu-s(p-1)-r}\, x_1^{p-r-1} x_2^{r}, \qquad (2)$$

where (K_ν) is the pure invariant

$$(K_\nu) = C_{p-1} + C_{2(p-1)} + \ldots + C_{(\sigma-1)(p-1)}. \qquad (3)$$

Now if we form the product of any two binary forms, as of f_m and

$$g_n = (b_0, b_1, \ldots, b_n)(x_1, x_2)^n \quad (m \geqq n),$$

where $m + n$ is a number of the form $\sigma\,(p-1)$, and construct the formulas analogous to (2), (3) for the result, we get

$$(f_m g_n) = \sum_{i=0}^{j(p-1)} \sum_{j=1}^{\sigma-1} a_i b_{j(p-1)-i},$$

$$[f_m g_n] = [a_0 b_0 + (f_m g_n)]\, x_1^{p-1} + \sum_{r=0}^{p-2} \sum_{s=0}^{\sigma-1} \sum_{i=0}^{t} a_i b_{(\sigma-s)(p-1)-r-i}\, x_1^{p-r-1} x_2^{r}$$

$$\{t = (\sigma - s)(p-1) - r\}.$$

This process of constructing the concomitants $(f_m g_n)$, $[f_m g_n]$ from the product $f_m \cdot g_n$ is analogous to transvection and symbolical convolution in the theory of algebraic concomitants.

An example of the covariant (1) is obtained from the following seminvariant[3] of a quadratic form f_2:

$$S = a_0^{p-1} a_1 - a_1^{p}.$$

This seminvariant satisfies the two necessary and sufficient conditions that it may be the leading coefficient of a covariant, viz., of [5c]

$$C_1 = (a_0 x_1 + a_1 x_2)^p - (a_0 x_1 + a_1 x_2)(a_0 x_1^2 + 2a_1 x_1 x_2 + a_2 x_2^2)^{p-1}, \qquad (4)$$

where powers of x_1, x_2 are to be reduced by Fermat's theorem.

2. Concomitant scales.—If K is any modular covariant of order $(rp - \nu) \times (p-1) = m$, then by application, to K, of the latter of the two modular invariantive operators [5b]

$$E = a_0^{p} \frac{\delta}{\delta a_0} + a_1^{p} \frac{\delta}{\delta a_1} + \ldots + a_m^{p} \frac{\delta}{\delta a_m},$$

$$\omega = x_1^{p} \frac{\delta}{\delta x_1} + x_2^{p} \frac{\delta}{\delta x_2},$$

there is obtained a set or scale of $\mu = p + \nu + 2$ concomitants

$$(K), \omega^{\lambda}[K]\ (\lambda = 0, 1, \ldots, p-1), \omega^{t} K\ (t = 0, 1, \ldots, \nu). \qquad (5)$$

This set, which we call a *μ-adic* scale[6] for K, is analogous to the set obtainable by convolution from a symbolical algebraic covariant

$$\Pi\,(ab)\, a_x^{p} b_x^{q} c_x^{r} \cdots.$$

A scale of modular concomitants is said to be *complete* when it contains all invariants and covariants of the first degree in the coefficients of K which can be obtained from K by empirical or modular invariantive processes, i.e. a *μ-adic* scale is complete when it constitutes a fundamental system of first degree concomitants of K. Thus we find that we are able to construct a complete modular system of a form f_m by a process of passing from a complete scale for f_m of the first degree to scales derived from covariants of f_m of degree > 1.

3. A complete system of the quadratic, modulo 3.—I have proved that the following eighteen quantics constitute a complete formal system modulo 3 of f_2; the proof resting primarily upon the fact that, when $p = 3$, every covariant is of even order, and hence the *μ-adic* scale (5) is complete:

$$\begin{aligned} &f_2,\ C_1,\ [f_2^2],\ [f_2C_1],\ [f_2^2C_1],\ Ef_2, \\ &\omega f_2,\ \omega C_1,\ \omega[f_2^2],\ \omega Ef_2,\ \omega^2 f_2,\ \omega^2 C_1, \\ &L,\ Q,\ (f_2^2),\ ([f_2^2]^2),\ (C_1Ef_2),\ \Gamma; \end{aligned} \tag{6}$$

where[3] $\Gamma = (a_0 + a_2)(2a_0 + 2a_1 + a_2)(2a_0 + a_1 + a_2)$, and L, Q are the functions to which the universal covariants of the group $G_{(p^3-p)(p^3-1)}$ reduce when $p = 3$. These covariants are[3]

$$L = x_1^p x_2 - x_1 x_2^p,\ Q = (x_1^{p^2} x_2 - x_1 x_2^{p^2})/L.$$

The last four quantics in the system (6) are pure invariants and constitute a complete system of invariants of f_2 modulo 3. This set of invariants was first derived by Dickson. The orders of the forms (6) range from 0 to 6 and the degrees from 0 to 6.

4. A complete system of the cubic, modulo 2.—When $p = 2$ the μ concomitants (5) do not form a complete scale. Every form of order > 3 is reducible[5c] modulo 2 in terms of invariants of the first degree in its coefficients and of its covariants of orders 1, 2 and 3. If K_ν is the covariant shown in §1 we have $(p = 2)$,

$$\begin{aligned} (K_\nu) &= C_1 + \ldots + C_{\nu-1}, \\ [K_\nu] &= [C_0 + (K_\nu)]x_1 + [(K_\nu) + C_\nu]x_2. \end{aligned}$$

These, and the additional covariant

$$\{K_\nu\} = C_0x_1^2 + (K_\nu)x_1x_2 + C_\nu x_2^2,$$

exist for all orders ν. When ν is odd there exists also a cubic covariant[5c]

$$\{\overline{K_\nu}\} = C_0x_1^3 + I_1x_1^2x_2 + I_2x_1x_2^2 + C_\nu x_2^3,$$

where I_1, I_2 are definite linear expressions in $C_1, \ldots, C_{\nu-1}$ such that[5d]

$$I_1 + I_2 \equiv (K_\nu) \pmod 2.$$

These concomitants, and their polars by $\omega = x_1^2 \frac{\delta}{\delta x_1} + x_2^2 \frac{\delta}{\delta x_2}$, form a complete scale for K_p.

A fundamental system of formal covariants of f_3 modulo 2 consists of the following twenty quantics;[5d] where we abbreviate by H the algebraic hessian of f_3, and

$$t = H + (f_3)\{f_3\}, \; l = Q[H] + f_3\,(f_3),$$

and in which L, Q are the universal covariants of the group G_6:

$$f_3, H, [f_3], \{f_3\}, Ef_3, E[f_3], \{f_3 t\}, \{Pt\}, [f_3 t],$$
$$[Ef_3 \,.\, t], \{\overline{f_3 t}\}, \{\overline{tEf_3}\}, [Ql], L, Q,$$
$$(f_3), (H), (tf_3), (tEf_3), I.$$

The invariant I, which is not represented as belonging to any scale, is

$$I = a_0^2 + a_0 a_6 + a_3^2 + (a_0 + a_3)(f_3).$$

The orders of the forms in this system range from 0 to 3, and their degrees from 0 to 4.

The proofs of the existence of $\{\overline{K_p}\}$ and of $[K_p]$ involve certain remarkable congruential properties of the binomial coefficients.[6]

Reduction methods rest largely upon the fact that two modular covariants of the same order and led by the same seminvariant, while not identical as a rule, are necessarily congruent to each other moduli $L\,(= x_1^{\,p} x_2 - x_1 x_2^{\,p})$, and p. Thus a covariant is not uniquely determined by its seminvariant leading coefficient as is the case with algebraic covariants. Another noteworthy general fact is that of the existence of covariants whose leading coefficients are modular invariants.

[1] Hurwitz, A., *Archiv. Math. Phys., Leipzig,* (Ser. 3), **5**, 1903, (17).

[2] Dickson, L. E., *Trans. Amer. Math. Soc.*, **10**, 1909, (123); **12**, 1911, (75); **14**, 1913, (290); and **15**, 1914, (497); *Amer. J. Math., Baltimore*, **31**, 1909; etc.

[3] Dickson, *Madison Colloquium Lectures*, 1913.

[4] Miss Sanderson, *Trans. Amer. Math. Soc.*, **14**, 1913.

[5] Glenn, O. E., (a) *Amer. J. Math.*, **37**, 1915, (73); (b) *Bull. Amer. Math. Soc., New York*, **21**, 1915, (167); (c) *Trans. Amer. Math. Soc.*, **17**, 1916, (545); (d) **19**, 1918, (109); (e) *Ann. Math., Princeton*, **19**, 1918, (201).

[6] A paper containing a portion of the general theory here mentioned and the derivation of the system of the quadratic modulo 3, as well as certain other developments, is to appear in *Trans. Amer. Math. Soc.*

THE GENERAL SOLUTION OF THE INDETERMINATE EQUATION: $Ax + By + Cz + \ldots = r$.

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Little has been done since Jacobi (*Werke*, **6**, 355) in connection with the solution of the general linear indeterminate equation. Jacobi has given no less than four methods all involving the reduction of the equation by means of a set of auxiliary equations to the solution of an equation in two variables the solution of which is immediately obtained from the theory of the ordinary continued fraction. The solution here presented treats the general equation in the same non-tentative way that is found in the continued fraction solution for two variables. The method applies equally well when the right hand member is zero and gives a perfectly general solution from which all other special solutions may be obtained.

Consider the set of positive or negative, non-zero integers $a_1, b_1, c_1, \ldots, k_1, l_1$ and let m be the number of terms in the set. We derive from this first set a second set $a_2, b_2, c_2, \ldots k_2, l_2$ by means of the equations:

$$\begin{aligned} a_2 &= b_1 - \alpha_1 a_1, \\ b_2 &= c_1 - \beta_1 a_1 \\ &\ldots\ldots\ldots \\ k_2 &= l_1 - \kappa_1 a_1, \\ l_2 &= a_1 \end{aligned}$$

where if a_1 is different from unity the numbers $\alpha_1, \beta_1, \ldots \kappa_1$ are so taken that $a_2, b_2, c_2, \ldots k_2$ are the smallest positive residues, not zero, of the numbers $b_1, c_1, \ldots k_1, l_1$ respectively with respect to the modulus a_1. If a_1 is unity then $\alpha_1, \beta_1 \ldots \kappa_1$ are taken equal to $b_1, c_1, \ldots l_1$ respectively, so that in this case the second set consists of zeros with the exception of the last term, l_2 which is unity.

We derive in the same way a third set from the second by means of the equations:

$$\begin{aligned} a_3 &= b_2 - \alpha_2 a_2 \\ b_3 &= c_2 - \beta_2 a_2 \\ &\ldots\ldots\ldots \\ k_3 &= l_2 - \kappa_2 a_2 \\ l_3 &= a_2 \end{aligned}$$

As in the preceding set, if a_2 is different from unity, we take the numbers $\alpha_2, \beta_2, \ldots \kappa_2$ so that $a_3, b_3, \ldots k_3$ are the smallest positive, non-zero residues of $b_2, c_2, \ldots l_2$ respectively, modulo a_2. If a_2 is unity, $\alpha_2, \beta_2, \ldots \kappa_2$ are taken equal respectively to $b_2, c_2, \ldots l_2$, and in this case the third set consists of zeros with the exception of the last, l_3, which is unity.

Continuing this process, if the original set had no common factor other than unity, we must arrive at a set in which the first number is unity. For it is clear that $a_{n+1} < a_n$ except when b_n is divisible by a_n in which case $a_{n+1} = a_n$. Further $a_{n+2} < a_n$ except when both b_n and c_n are divisible by a_n, in which case $a_{n+2} = a_{n+1} = a_n$, and so on. If now the original set had the greatest common divisor unity so will also the set $a_n, b_n, c_n, \ldots k_n, l_n$, and so not all the numbers $b_n, c_n, \ldots k_n, l_n$ can be divisible by a_n. After a number of steps in the process at most equal to $n - 1$ an a_λ must appear which is less than a_n and not zero. In the same way another set must appear in which the first number is less than a_λ and so on. This process must then lead to a set in which the first number is unity. By taking one more step a set is then obtained in which the numbers are all zeros except the last which is unity.

We proceed now to reverse the above process, and taking the numbers $\alpha_1, \beta_1, \ldots \kappa_1$: $\alpha_2, \beta_2, \ldots \kappa_2$: $\ldots$ as given we will show how to reconstruct the original set $a_1, b_1, c_1, \ldots k_1, l_1$ from them. We construct first a determinant of order m in which the element of the prinicipal diagonal are all units, and all the other elements are zero. Using the first set of numbers $\alpha_1, \beta_1, \ldots \kappa_1$, which we will call the first 'partial quotient set' we construct what we will call the 'first determinant' as follows: The top row of the above determinant is erased and another row is added at the bottom which has for its elements $1, \alpha_1, \beta_1, \ldots \kappa_1$. This bottom row we will call the first 'convergent set' and for uniformity of notation we write it $A_1, B_1, C_1, \ldots K_1, L_1$. It is seen that the value of the first determinant is unity.

Using the second partial quotient set, $\alpha_2, \beta_2, \ldots \kappa_2$. we obtain from the first determinant a second determinant by erasing the top row and adding for the bottom row the second convergent set $A_2, B_2, C_2, \ldots K_2, L_2$, the elements of which are obtained by adding the columns of the first determinant after multiplying the first row by 1, the second by α_2, the third by β_2, etc. and the bottom row by κ_2. In the same way we get the third determinant and the third convergent set, using the third partial quotient set $\alpha_3, \beta_3, \ldots \kappa_3$. The nth convergent set, which is the bottom row of the nth determinant is related to the preceding sets by the recursion formulae:

$$A_n = \kappa_n A_{n-1} + \ldots \alpha_n A_{n-m+1} + A_{n-m}$$

with similar formulae for the B_n, C_n, etc. It is clear from the way the determinants are derived from each other and from the original determinant that the value of each is unity.

We state now the remarkable theorem that the last convergent set is identical with the original set $a_1, b_1, c_1 \ldots k_1, l_1$, from which the successive partial quotient sets were derived. This theorem comes out of the general theory of continued fractions, of multiplicity m, but without any appeal to that theory Professor Frank Irwin has derived it very simply from the following equations which are easily established by complete induction:

$$a_1 = a_nA_{n-m} + b_nA_{n-m+1} + \ldots k_nA_{n-1} + l_nA_n \qquad n = 1, 2, \ldots$$
$$b_1 = a_nB_{n-m} + b_nB_{n-m+1} + \ldots k_nB_{n-1} + l_nB_n \qquad A_0 = A_{-1} = A_{-2} =$$
$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \qquad \ldots = A_{-m+1} = 0,$$
$$l_1 = a_nL_{n-m} + b_nL_{n-m+1} + \ldots k_nL_{n-1} + l_nL_n \qquad A_{-m} = 1, \text{ etc.}$$

Now, as we have seen, in the last set a_n, b_n, c_n, k_n are all zero, and l_n is equal to unity. This gives the theorem.

This theorem throws into our hands a straightforward method of writing down a determinant equal to unity whose bottom row is any given set of positive or negative non-zero integers, with greatest common divisor unity. Let this last row be A_n, B_n, C_n, . . . K_n, L_n, and let the co-factors of these elements in the last determinant be A'_n, B'_n, C'_n, . . . K'_n, L'_n. Then these co-factors furnish a set of values for the unknown in the indeterminate equation $A_nx + B_ny + \ldots L_nv = 1$, and by multiplying these values through by r we get a solution of the equation when the right member is equal to r. Moreover since $A_nA'_\rho + B_nB'_\rho + C_nC'_\rho + \ldots K_nK'_\rho + L_nL'_\rho = 0$ for $\rho = n - 1, n - 2 \ldots n - m + 1$ we may write for the most general value of the variables:

$$x = rA'_n + sA'_{n-1} + tA'_{n-2} + \ldots \qquad + pA'_{n-m+1} + qA'_{n-m}$$
$$y = rB'_n + sB'_{n-1} + tB'_{n-2} + \qquad pB'_{n-m+1} + qB'_{n-m}$$
$$z = rC'_n + sC'_{n-1} + tC'_{n-2} + \qquad + pC'_{n-m+1} + qC'_{n-m}$$
$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

That this is the most general form of the solution follows from the fact since the determinant of the co-factors is unity a set of integer values of $r, s, t, \ldots p, q$ can always be found for any given set of values of $x, y, z, \ldots$

We give as a numerical example the problem of determining the most general solution of the indeterminate equation:

$$33x + 55y + 79z - 99w = r.$$

The following is a convenient arrangement of the work of computing the sets a_1, b_1, c_1, d_1, α_1, β_1, γ_1, etc.

a_n	b_n	c_n	d_n	α_n	β_n	γ_n
33	55	79	−99	1	2	−4
22	13	33	33	0	1	1
13	11	11	22	0	0	1
11	11	9	13	0	0	1
11	9	2	11	0	0	0
9	2	11	11	0	1	1
2	2	2	9	0	0	4
2	2	1	2	0	0	0
2	1	2	2	0	0	0
1	2	2	2	2	2	2
0	0	0	1			

With these values of $\alpha_n, \beta_n, \gamma_n$ we proceed to compute the successive convergent sets and the corresponding determinants. The following is a convenient arrangement of the work:

			A_n	B_n	C_n	D_n
			1	0	0	0
			0	1	0	0
			0	0	1	0
α_n	β_n	γ_n	0	0	0	1
1	2	−4	1	1	2	−4
0	1	1	1	2	2	−3
0	0	1	1	2	3	−3
0	0	1	1	2	3	−2
0	0	0	1	1	2	−4
0	1	1	3	5	7	−9
0	0	4	13	22	31	−39
0	0	0	1	2	3	−2
0	0	0	1	1	2	−4
2	2	2	33	55	79	−99

The last determinant yields us the solution of the proposed problem. Computing the minors we easily get the following general values for the unknowns in the equation:

$$x = -29r - 57s + 54t - 65u$$
$$y = 3r + 4s - 4t + 7u$$
$$z = 5r + 11s - 11t + 11u$$
$$w = -4r - 8s + 7t - 9u$$
$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

THE ARCHAEOLOGY OF THE SOUTHWEST: A PRELIMINARY REPORT

By N. C. Nelson

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Communicated by Henry F. Osborn, February 6, 1919

Introductory.—Since my last communication to the Proceedings of the National Academy (Vol. 3, pp. 192–195) two years ago, concerning the time distribution of aboriginal traits in the Mammoth Cave region of Kentucky, it has become possible to report upon the stratigraphic conditions in two additional North American culture centers. One of these new centers, viz., the Florida-Georgia characterization area, directly adjoins that in which the Mammoth Cave occurs, in fact is in a large sense one with it and need not therefore be specifically discussed. The other center, of special concern here is sepa-

rated from the preceding by the totally different Plains culture area and lies in the semi-arid plateau region known culturally as the Pueblo area and geographically as the Southwest. The mentioning of these three distinct and partly separated centers together in this place is made possible and necessary by the fact that our archaeological findings in them are identical in their general import, as will be brought out at the end of the discussion.

The Pueblo culture area is from several standpoints our most profitable field for the study of primitive man. It is to us what Egypt is to the Old World and more. For not only have we here an abundance of ruins more or less ancient but we have the relatively unspoiled descendants of the builders still surviving, and we have documentary data concerning them reaching back nearly four hundred years. It is a field therefore in which the ethnologist, the historian, and the archaeologist can work hand in hand; and, needless to say, they have done so. Each mode of approach has, however, its particular limitations; and it has of late become evident that an adequate solution of the problem presented lies in a coordination of effort. The ethnologist, e.g., sees the problem clearly only in its spatial dimension; the historian makes a brief beginning with the time projection but to complete his work he must of necessity appeal to the archaeologist. The archaeologist, on the other hand, while he may see the problem in both dimensions, unless already an ethnologist, is obliged to call upon such a specialist to assist him in the interpretation of his findings. The failure to fully appreciate these interrelations will probably in a large measure explain the history of anthropological investigation in the Southwest.

History of Archaeological Investigation.—The Pueblo culture area has been under consideration for seventy-three years and something like three stages are discernible in the process. Of the numerous reports now available on the antiquities, those of the first thirty years were written by staff members of various governmental expeditions and surveys and were of a general descriptive character. About 1880 the investigation became institutionalized, so to speak. Specialists in history, ethnology, and archaeology entered the field and all have delivered more or less convincing reports on the problem from their particular points of view. But, naturally enough, only the historian has in any sense finished his task. The ethnologist has his work well under way; while as for the archaeologist—in spite of all he has done and written—his results have not until lately been carried much beyond the analytic stage. During the last few years finally there has been a distinct effort on the part of several investigators to reach the synthetic level or in other words to get beyond the descriptive and classificatory routine work to really interpretative results. It is pleasant in this connection to be able to say that the American Museum's archaeological work, prolonged now for seven years and taken part in by Messrs. Leslie Spier and Earl H. Morris as well as the writer, has been primarily of this interpretative character. We have entered the field not so much to recover specimens as to solve problems. Owing to the immensity of the

field we have, however, like other investigators, been compelled to begin with merely local problems; but the solution of these local problems has—so we believe—led to the discovery of simple methods applicable to the Pueblo problem in its entirety.

The Field Data.—The Pueblo Indians, in the light of the ethnological and historical information we have concerning them, may be defined as a group of sedentary tribes who build substantial rectangular houses of a more or less compact and communistic type, who commonly construct semi-subterranean ceremonial chambers, either round or rectangular, who build reservoirs and irrigation ditches, who grow corn, beans, and squashes for food as well as cotton for clothing, who grind their corn on a metate, who use the curved rabbit-stick and the tubular pipe, who possess a special type (or types) of grooved ax, who work turquoise and who make pottery having very striking local peculiarities. The ethnologist would indicate additional characteristics of a linguistic, social, and religious nature; but these because they have received less definite or permanent material expression are of secondary importance to the arachaeologist as working data. Some of the cited traits, like maize growing, the Pueblo share in common with other and even very distant tribes of North and South America; certain other traits like the round ceremonial chamber are only partially diffused over their own territory; and still other traits, like cotton growing and the stone ax, have completely disappeared in modern times. Perhaps the most characteristic of the surviving traits, considered both as geographical and as historical phenomena, are architecture and ceramics.

The tribes who today exhibit the above characters are domiciled in about thirty villages specifically known as *pueblos* in contradistinction, first, to the less local, rather loosely constructed and only semi-permanent type of villages known as *rancherias* and, second, to the still more widespread temporary settlements known as *camps*. Their numerical strength, according to the last census is about 11,000 souls; and their territorial possessions, in the form of land grants and reservations, are officially placed at about 5,000 square miles. These artificial boundaries are not exactly conterminous with the actual range of the tribes but the figures give a fair idea of the amount of territory from which they draw sustenance.

In 1540 or thereabouts when the Spanish explorers first entered the country the Pueblo appear to have inhabited all of seventy villages and to have numbered about 20,000, a few more or less. Their territorial range was about 13,000 square miles, or more than twice what it is today, a large section having been vacated, e.g., on the southeast. That much is determined for us in part by the historian; but from this point on for another short stretch only the ethnologist can accompany us.

After several decades of more or less desultory work we are now in position to say that the Pueblo in prehistoric times ranged over a territory little short of 140,000 square miles in extent, throughout which they have left ruins and other characteristic remains very similar to those found in the territory still

occupied. Beyond this territory, finally, there is a wide marginal zone, which taken together with the central area is little short of 1,000,000 square miles in extent, and throughout which appear ruins and remains in some respects like those of the Pueblo area proper and in other respects like the remains characteristic of Nomadic regions, i.e., essentially 'rancherias.' In short, the geographic distribution of Pueblo traits takes the form of a *center* of high and unalloyed development and a *marginal zone* different segments of which have been more or less affected by influences from other adjacent culture centers. The bearers of the pure Pueblo culture still reside in the heart of the old center; and several tribal groups of the hybrid Pueblo-Nomad type also continue to reside in the western and southern portions of the marginal zone. Lastly, several slightly modified but vigorous strains of nomadic cultures are present on the north and southeast, not only in the marginal zone but in considerable stretches of what was once pure Pueblo domain. The spatial condition of affairs is diagrammatically represented in figure 1.

On the face of it the diagram indicates two things: first, a tremendous geographical concentration of the pure Pueblo culture or as we might just as well say, a falling off in Pueblo influence; and, second, and what amounts to the same thing, several great nomadic invasions which have swallowed up or pressed back the Pueblo traits on the north and southeast and all but detached several small marginal centers on the south and west. After several years of contact with the facts of this situation the writer is unable to escape the conclusion that they are all very intimately connected and that either set of them largely explains the other. At this point, then, we have to leave the ethnologist behind: if we wish to know anything further we have to dig below the surface. Given the spatial phenomenon presented in our diagram, it is for the archaeologist to present the same set of facts as a time phenomenon, in other words, to arrange the data in their proper historical sequence. And to do this he must devise adequate methods of his own.

Concerning Methods.—One of the difficulties that the archaeologist has labored under has been the mass of the data confronting him. In his effort to master details he has lost touch with the problem as a whole. No one man has yet seen the entire field with his own eyes. Dr. J. W. Fewkes, who may be said to have initiated the last phase of the investigation, has, e.g., done his work largely in the western sector and has generalized on the problem from that point of view, using mainly architectural traits as a basis. Dr. A. V. Kidder has worked mostly in the northern sector and has generalized mainly on the basis of ceramic traits. Both employed the method of direct comparison. The writer finally has done his work chiefly in the southeastern sector, using ceramics as a medium and employing as a method, in addition to that of direct comparison, the simple principle of stratification. Resort to this medium and to this principle came about in a very natural manner.

The data we have to deal with consist of some six or seven hundred major, i.e., pueblo, ruins of various types, located within our center of high develop-

ment; and, in addition, an untold number of minor ruins, partly of the rancheria type, scattered over both the Central area and the great Marginal zone. The immediate problem confronting the archaeologist has been to decide whether these ruins were chronologically separable. Until recently the general verdict has been that they were not, except of course within the narrow limits of 'historic' and 'prehistoric.' A third and intermediary group we may perhaps concede to have been detached on the basis of traditional references to it, but that is all. Our prehistoric ruins were simply 'prehistoric,' that is, roughly speaking, they were of the same age: and the result has been some extraordinary speculations about great numbers of peoples and their mysterious disappearance, which has finally been credited by some to a fancied 'change of climate.'

Unfortunately, the appearance of the ruins was no criterion of age. Neither did the achitecture as architecture give away in a really clear manner the order of development, doubtless partly because architecture is in a large measure determined by environmental conditions. Pottery—an ever present accompaniment of the ruins—is on the other hand, an exceedingly plastic phenomenon, varying from place to place and from time to time, in response to the inventive faculty, far more readily than does architecture. We may therefore decide the relative age of any given ruin by determining the age of the particular style of pottery which it exhibits; and this latter feat is easily accomplished. We have but to find the stratigraphic position of this particular style in the total series of styles as they occur in refuse heaps or in actually superposed ruins. Sometimes the stratigraphic position has to be determined without digging into the refuse heaps—there being none, but the principle involved is the same: we have to begin with the style of ware lying on top or still in use and must work back or down through the series until we arrive at the bottommost style, which is the oldest. We may indicate our general procedure therefore by saying that instead of as formerly hunting out the most picturesque ruins for excavation or at any rate the ruins giving promise of the finest outlay of specimens, we have begun commonly with the despised ruins of historic date situated in the heart of the present Pueblo habitat.

Results to Date.—Our method has not yet been applied to the entire Pueblo area and consequently our results are not complete in respect to numerous details. Nevertheless, the general outline of things, i.e., the chronological disposition of the ruins, is already tolerably clear and has been diagrammatically represented in figure 2 which is, as it were, a section in the A-B line of figure 1. To date we have, so to speak, dug down through the superposed culture levels found in both the Zuni and the Tewa circles, in fact through several additional but more ancient circles not presented in the diagram. By thus discovering the time order of things we have with the same effort discovered the key to the whole spatial arrangement. For as we dig down through the vertical series we pass gradually from Pueblo to Rancheria traits and from Rancheria to Nomadic traits exactly as if we were traveling from the present center of Pueblo life out over the various zones to the Nomadic border. Briefly, it is archaeolog-

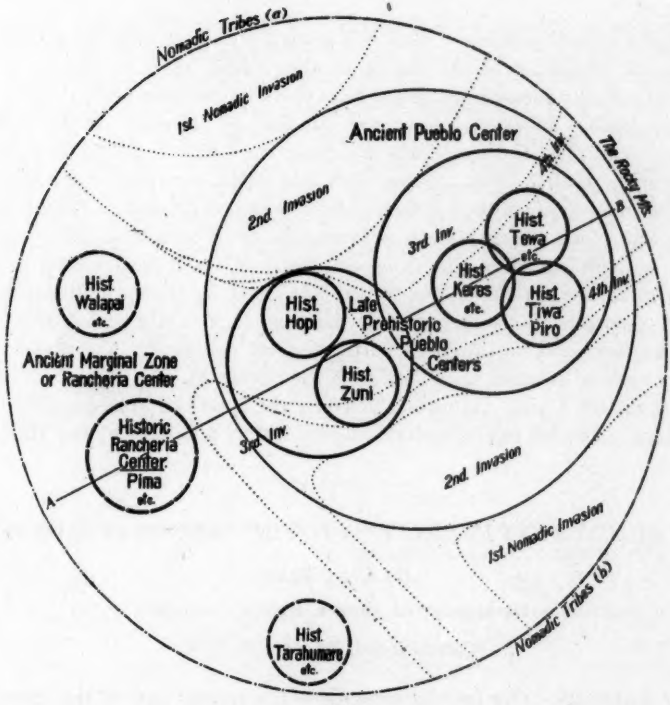

Fig 1.

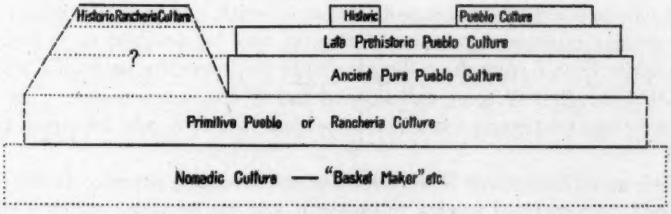

Fig 2.

FIG. 1. SPATIAL DISTRIBUTION OF PUEBLO TRAIT GROUPS

FIG. 2. TIME DISTRIBUTION OF PUEBLO TRAIT GROUPS, IN A-B LINE OF FIGURE 1

ically demonstrable, as perhaps many will say they knew long ago, that the Pueblo culture grew out of a Nomadic one.

Conclusions.—There is no space here for the discussion of details. There remains to add however that it is not clear whether the Pueblo phenomenon is something altogether special in culture or whether in reality it is a fine illustra-

tion of a general principle. That is, I am not certain whether the accident of Nomadic invasion produced the outstanding Pueblo traits or whether in the absence of such pressure we should have observed the same phenomenon in all its essentials. In short, does or does not the 'age and area' hypothesis, commonly subscribed to by students of organic life, hold true also in the province of human culture? But, passing over that detail, one thing seems fairly established both here in the Southwest and in several of our eastern culture areas. It is that North America north of Mexico, before it became settled by sedentary agricultural tribes who developed many of the traits common to that type of life the world over, was settled by a generally more primitive nomadic type of peoples subsisting mainly by hunting, such as still persist over all of the northern and northwestern portions of the continent. The above summary account is based upon data from the Archer M. Huntington Survey of Southwestern United States conducted by the American Museum of Natural History. The full report upon this survey will be published by the Museum.

AN ADJUSTMENT IN RELATION TO THE FRESNEL COEFFICIENT[1]

By Carl Barus

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Communicated, February 10, 1919

1. Apparatus. One internal reflection.—The specific part of the apparatus is the glass cylinder, G, figure 1, with a carefully polished mantel, capable of rotating around an axis, A, normal to the ray-plane of the interferometer.

If micrometer facilities are to be dispensed with, and that is permissible in the present experiment,[2] the interferometer may be designed as in figure 1. The white light L from the collimator takes the respective paths $dCC'd'b$ and $bd'C'Cd$, the plate N being half silvered and N' an opaque mirror. The telescope or spectro-telescope is at T. The glass face at N may be turned either way.

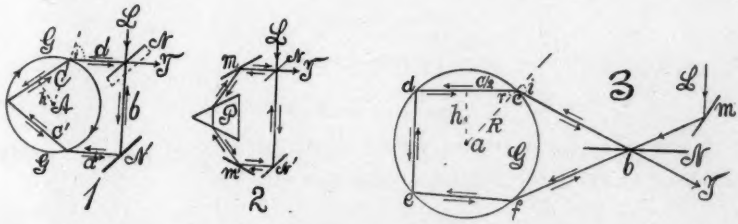
Such an interferometer is self adjusting (cf. preceding paper). In the form, figure 1, two reversed spectra will be visible in the telescope, which if superimposed by rotating N or N' on a vertical axis, will show the linear phenomenon at once, in any color at pleasure. The fringes may be enlarged by rotating N or N' on a horizontal axis and they are symmetrically equal in size on the two sides of the adjustment for infinitely large fringes.

If the achromatics are wanted, a prism must be inserted into the rays b (preferably) between N and N', with a prism angle and other conditions selected to counteract the refraction of the cylinder G.

2. Apparatus. Two internal reflections.—As the fringes were found without much difficulty (§5) in case of one internal reflection, it seemed desirable

to ascertain whether this would still be feasible in the apparently more favorable, but also more difficult case of two internal reflections. In figure 3, white light arrives from a collimator at L and strikes an auxiliary mirror m, before reaching the half silver N. If m is capable of rotating both on a horizontal and vertical axis as well as sliding right and left in the diagram, it greatly facilitates adjustments of angle and location of rays. The two beams *bcdef* and *bfedc* reunite at b after passing the glass cylinder G (rotating around the axis a) and are observed by the telescope at T. As the spectra (after refraction at c and f) are reflected 3 and 2 times respectively, the fringes of non-reversed spectra will be obtained covering the whole length of spectrum. A glass G of low index of refraction will here usually be preferable.

In case of a half silver mirror at a small glancing angle there are usually two pairs of bright spectrum images, and one fainter pair, apart from very faint ones. One bright and one faint pair carry identical fringes and the spectrum images may be small enough to be separated. In case of clear



glass, however, there is practically but one pair of bright images, and they carry fringes when properly superposed.

3. Equations.—The first question to be elucidated is the nature of the conditions of refraction. From the figure, in view of the symmetry of the arrangement, if b is the breadth of the ray parallelogram and R the radius of the cylinder, μ its index of refraction, h the distance of the chord C from the axis A, i and r the angles of incidence and refraction of the rays dC or $d'C'$:

$$\sin i = \sin 2r = b/2R \tag{1}$$

$$\sin r = h/R \tag{2}$$

$$\mu = 2 \cos r = b/2h \tag{3}$$

The relations remain the same if $b/2r$ is constant. If the (small) value b = 10 cm. is inserted into the equation, the conditions may best be shown by a graph for i and μ. It will then be seen that for diameter $2r$ between 10 and 11 cm., the available indices of refraction of the glass would increase from 1.4 to 1.7 roughly, while the angle i falls from 90° to about 65°. Hence the experiment requires the interfering rays to impinge near the outer limits of the cylinder.

It is next in order to consider the possibly observable conditions of the (apparent) ether drag. The velocity within the refracting medium of index μ is usually written (or follows from the theory[3] of relativity) in the form

$$c/\mu \pm v\,(1 - 1/\mu^2) \tag{4}$$

where v is the velocity of the medium in the direction, or contrary to the direction of the velocity of light c. It remains to determine the average speed of the beam along the chord C of figure 1. From the figure

$$C = \mu R \text{ and } b = 2\mu h \tag{5}$$

whence

$$b = 2\mu R \sqrt{1 - \mu^2/4} \tag{6}$$

In figure 1 let ω be the angular velocity of the cylinder G and dx an element of the chord C at a distance ρ from the axis A. Let the minimum distance of this chord from A be h and θ its angle with ρ.
Then

$$dx = \rho^2\,\omega\,dt/h,$$

if dx is described in the time dt. Hence

$$dx/dt = \omega\,(h^2 + x^2)/h \tag{7}$$

To find the mean speed v along C, we may multiply dx/dt by dx, integrate between 0 and $C/2$ and divide the result by $C/2$. Thus

$$v = \omega\,(h + C^2/12h) \tag{8}$$

Reducing this equation by (1), (2), (5), eventually

$$v = R\omega\,\frac{1 - \mu^2/6}{\sqrt{1 - \mu^2/4}} \tag{9}$$

or the mean speed along C may be expressed in terms of R, ω, μ, while v is naturally proportional to R and ω

The ratio of the speed in equation 9 (seeing that it is respectively + and − for the two interfering rays) to the velocity of light is thus $2v/c$. Since these rays traverse a path $2C$ in the rotating cylinder in opposite directions the path difference resulting will be

$$\Delta P' = (2v/C)\,2C = 4Cv/c = \frac{4\mu\omega R^2}{c}\,\frac{1 - \mu^2/6}{\sqrt{1 - \mu^2/4}} \tag{10}$$

so that the path difference for a given μ and ω increases with the square of the radius, R, of the cylinder or disc.

But the equation (4) introduces another factor $(1 - 1/\mu^2)$ so that finally the path difference is

$$\Delta P = \frac{4\omega R^2}{c} \frac{\mu\,(1-\mu^2/6)\,(1-1/\mu^2)}{\sqrt{1-\mu^2/4}} \tag{11}$$

We may now take the above case ($b = 10$ cm.) from the graph i, μ, for a small cylinder, making 100 turns per second.

$$R = 5.3 \text{ cm}; \mu = 1.63; \omega = 628; i = 70.6°; r = 35.3°; b = 10 \text{ cm}.$$

In accordance with equation (10), therefore, the uncorrected path difference is

$$\Delta\ P' = 2.95 \times 10^{-6} \text{ cm}.$$

and the corrected path difference finally,

$$\Delta\ P = 1.84 \times 10^{-6} \text{ cm}.$$

The fringes which appear in the above interferometer are primarily those of reversed spectra. If the yellow parts of the spectra ($\lambda = 60 \times 10^{-6}$) are superposed, 0.031 of a fringe would pass for the given radius of cylinder ($R = 5.3$ cm.) at 100 turns. A cylinder 30 cm. in diameter (about a foot) would therefore show .28 fringe, and since this may be doubled by reversing the rotation of the cylinder, (by which strains due to centrifugal force are also eliminated) something short of $\frac{3}{4}$ of a fringe should be observed.

With an ocular micrometer divided in 1/10 millimeter, it should be possible to secure fringes as much as 3 mm. apart, so that a displacement of 20 scale parts may be expected, ten for each of the directions of rotation.

4. Equations. Two reflections.—The equations for this case are somewhat more involved than the preceding; but it suffices to accept for the angle of incidence i at the cylinder G, figure 3, the value given by the old-fashioned theory of the rainbow; viz.,

$$8 \cos^2 i = \mu^2 - 1 \tag{12}$$

The chord C from c to d, etc., and its distance h from the axis a will be, as before, $C = 2R \cos r$, $h = R \sin r$, where r is the angle of refraction and R the radius of the cylinder. Finally equation (8), for the average speed v along a chord, also applies. Hence with the inclusion of equation (4), the path difference on rotation may be written, c being the velocity of light,

$$3 \times 2\ C\ (v/c)\ (1 - 1/\mu^2) \tag{13}$$

since there are three chords, C, in sequence. This expression may be reduced by the equations for C, h, v, and equation (12), eventually to a form convenient for computation.

$$(9R^2\omega/c)\ (3/\mu^2 + 1)\ \sqrt{(1-1/\mu^2)/(9/\mu^2-1)}$$

Data similar to the above may now be inserted; viz., for a small cylinder of water (to be used in the experiments below)

$$R = 5 \text{ cm.}; \mu = 1.33; \omega = 628; c = 3 \times 10^{10}$$

whence the path difference 1.82×10^{-6} cm. results.

This, curiously enough, is about the same value which was obtained in case of equation (11), so that identical deductions apply. The conditions are somewhat more favorable for larger values of μ. Thus in the limiting case $\mu^2 = 3$, the path difference would be about doubled.

5. Experiments.—To carry out these experiments at the present time is of course out of the question; but a number of contributory observations may be made with advantage. The case of figure 2 is similar to figure 1, where the dispersion of the cylinder G in the former case is simulated by the prism P and the auxiliary mirrors m, m', of the latter. If the slit of the collimator at L is not too coarse, two reversed spectra will be seen in the telescope at T, which on being superposed by rotating m or N on a vertical axis, will show a vivid linear phenomenon in the line of symmetry of the two superposed spectra. On rotating m or N on a horizontal axis, the distance apart of the fringe dots along this line may be given any reasonable value, at pleasure. These displacements are at once referred to the definite wave length in which the linear phenomenon is put. The dispersion of the prism has no bearing on the clearness of the phenomenon: 30° and 60° prism were tested with like results.

To obtain the achromatics and increased luminosity in the spectrum fringes (now to be horizontal bands throughout from red to blue), the rays of the spectrum will have to be reassembled and that may be done by inserting a second prism say P', between L and N', in a way to counteract the effect of the first. If the achromatics are to be obtained, the glass paths of the two rays in P and P', respectively, must be coincident. Hence, the axis of the collimator at L must be inclined to accommodate the angle of minimum deviation of the identical prisms P, P'; and while N and m are parallel, N' and m' normal to each other, L and T have their axes symmetric to N. The adjustment is not difficult as they need not be perfect to secure good achromatics; but if it is not made the fringes are numerous, colored, and unsatisfactory.

The experiments, figure 2, differ from the case figure 1, because the rays are parallel in the former case and condensed to a caustic by the eccentric refraction of the cylinder in the latter. Hence with these a short range telescope with strong objective is necessary; but as has been stated, the lines of the solar spectrum nevertheless come out clearly. Experiments were therefore made by simulating the glass cylinder GG by a thin cylindrical glass shell, closed below and above and containing a solution of mercury potassic iodide with an index at pleasure between 1.5 and 1.7. It was not difficult to meet the conditions of figure 1 so far as mere refraction is concerned, and certain incidental results obtained in this work have been given elsewhere.

The active slit in this experiment is the image within the cylinder, of the slit of the collimator and the former is sufficiently fine to show the Fraunhofer lines, even when the latter is a millimeter broad, so that there is no deficiency of light.

But in relation to the detection of the interferences, the two reversed spectra, strongly divergent in their homogeneous rays, introduce certain grave difficulties. For it will appear that the spectrum issuing at d', figure 1, passes over the distance b further than the spectrum issuing at d, before they reach the telescope together. The result is that the apices of two spectra lie in different focal planes, unless the telescope T is very remote. This makes the adjustment difficult.

To obviate this annoyance a symmetrical adjustment, with an additional mirror at d, figure 1, corresponding symmetrically to N and a symmetrically placed cylinder G, is here preferable. In such a case the spectra lie in the same focal plane, and since they have undergone 2 and 3 reflections, respectively, before reaching T, the interferences of non-reversed spectra are obtained without much difficulty. In my experiments, owing to the irregularity of the glass cylinder used, the fringes were correspondingly irregular; but otherwise clear and strong, as a wide slit is admissible.

The case of two internal reflections is complicated by the occurrence of multiple images from N, figure 3, even when one side is half silvered. This is particularly the case when the cylinder G contains water, as in my first experiments; for the glancing angle at b is then but 25°. There is an advantage, however, inasmuch as N may be placed at a correspondingly large distance from G. In spite of the duplicated images, the fringes were found more easily and were less irregular than anticipated. They are liable to be reproduced usually in a different size and orientation in each of the images. They will be found in the colored edge and even in the white glare (caustic) which emanates from the cylindrical surfaces. They could be made quite large, clear and strong, moreover, although the cylinder used was (as above) an ordinary glass shade. As in case of the triangular interferometer, the fringes rotate when N is displaced parallel to itself on the micrometer screw. To control their size N is to be rotated on a horizontal axis.

[1] Advance Report from the Carnegie Publications of Washington, D. C.

[2] With regard to the symmetrical interferometer form, cf. Michelson and Morley, *Amer. J. Sci., New Haven*, **31**, 1886, (377), also Zeeman, below.

[3] The insufficiency of this equation has been shown by Zeeman, *Proc., Amsterdam Acad.*, September 1914, and September 1915. But an estimate only is above in question.

PIEBALD RATS AND THE THEORY OF GENES

By W. E. Castle.

Bussey Institution, Forest Hills, Boston, Mass.

Communicated February 26, 1919

The study of heredity as an exact science dates from the rediscovery of Mendel's law in 1900. After the validity of the law had been established by abundant and conclusive evidence, the question arose, are the gametes pure. Is a character which disappears in crosses, and then reappears a generation later in 25% of the offspring, subject to contamination or modification during the process? The idea of gametic purity was at first looked on with favor. Bateson[1] although he never gave unqualified adhesion to this view, formulated it very clearly, thus. "The pure [homozygous] dominant and the pure recessive members of each generation are not merely like, but identical with the pure parents, and their descendants obtained by self-fertilization are similarly pure. If they are pure, surely the male and female elements of which they were composed must also be pure."

My own experimental studies of heredity, begun in 1902, early led me to observe characters which were unmistakably *changed* by crosses and so I have for many years advocated the view that the gametes are not pure in the sense expressed by Bateson. Moreover it was observed that characters which mendelize in crosses may, even when uncrossed, show fluctuating or graded variation in consequence of which systematic selection is able to produce very diverse races as regards a single mendelizing character, the ordinary allelomorph of which is wholly excluded from the experiment. This observation shows that characters may vary otherwise than by contamination and I was in consequence led to adopt the hypothesis that unit-characters are "inconstant" in varying degrees, but probably never perfectly constant.

This view has been repeatedly challenged, either by those who questioned the evidence cited in support of it, or by those who first substituted a different concept, 'gene,' for that of 'unit-character' and then denied that a 'gene' can vary. Dissent to the evidence for character variability has gradually disappeared as others have independently undertaken to study the visible characters of organisms as affected by crossing or systematic selection. The findings are commonly such as I have described in the case of the hooded pattern of piebald rats, which I have been studying for several years. This pattern is a simple recessive in crosses with the self pattern of wild rats, but it usually emerges from such crosses in a modified form, the amount of white in the pattern being either increased or diminished according to what stock is selected for experimental study. Even when uncrossed and bred as pure as possible, I have always found a certain amount of genetic variability to persist in a hooded race, so that selection, plus or minus is effective in changing it. The

facts as I have described them are now pretty generally accepted as correct, but two different views as to their interpretation have been suggested, both of which can not be true. These two views were outlined by Castle and Phillips[2] when the first part of the experimental data was published. We considered the evidence then in hand inconclusive as between the two interpretations and planned experiments to yield, if possible, decisive evidence for one or the other. This evidence is now complete, but before I undertake to summarize it, I wish to outline the alternative interpretations to be tested. They center about the concept of the 'gene,' to which reference has already been made. The term gene or gen was introduced by Johannsen in an attempt to simplify the ideas involved in the previously current term, unit-character. By unit-character was understood (1) any visible character of an organism which behaves as an indivisible unit in Mendelian inheritance and (2) by implication, that thing in the germ-cell which produces the visible character. Johannsen[3] pointed out that these two things were logically distinct, suggested the term gene for the hypothetical germ-cell determiner, and made it clear that it is not possible to say how many germinal determiners (genes) are involved in the production of a single visible character, but only how many are present in alternative forms (as allelomorphs). He therefore advised the entire discontinuance of the use of the term unit-character and proposed to discuss the subject of heredity exclusively in terms of genes. This is the so-called genotype theory.

Before this theory could be accepted unreservedly, it has seemed desirable to know whether all observed inheritance phenomena can be expressed satisfactorily in terms of genes, which are supposed to be to heredity what atoms are to chemistry, the ultimate, indivisible units, which constitute gametes much as atoms in combination constitute compounds. It also seemed desirable to know whether a single gene is indeed invariable like an atom (or a simple chemical compound).

Much study has in recent years been given to these questions with the result that (1) to express all heredity in terms of unvarying genes, it is necessary to suppose that besides the single gene indispensable to the production of a visible character, its gene proper, there occur also other genes whose action is subsidiary. Their action may not be indispensable to the production of a character, yet they certainly modify its visible form. These are called modifying genes. In some cases they are known to have other functions also. Thus the gene proper of one character may function also as a modifying gene for another character. But in the majority of cases the only ground for hypothecating the existence of modifying genes is the fact that characters are visibly modified.

As an alternative to the theory of modifying genes, the theory has been considered that genes may themselves be variable and if so, genes purely modifying in function might be dispensed with.

These are the alternative views that we had in mind in our experiments with the hooded character of rats. It had been established that the hooded character varied but that it gave unifactorial inheritance ratios. The question to be determined was whether the single gene plainly in evidence was or was not variable. To test the point it was necessary to make the 'residual heredity' as nearly constant as possible, whether this consisted of modifying genes or not. For the purpose of determining whether the gene proper for the hooded character had or had not varied in the course of our selection experiments, we proposed to utilize two very diverse races of hooded rats produced by many generations of selection in opposite directions. They were (1) *a plus selected race* in which the pigmented areas had been increased as much as possible by selection, and (2) *a minus selected race* in which the pigmented areas had been reduced as much as possible by selection, both having been derived at the out-

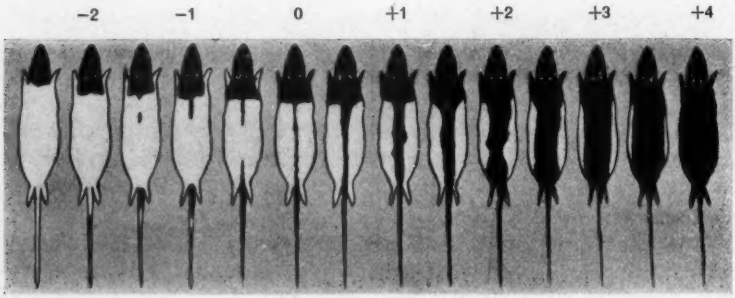


FIG. 1. A SET OF "GRADES" USED IN CLASSIFYING THE OBSERVED VARIATIONS OF THE HOODED CHARACTER OF RATS

Pictures at the extreme right and extreme left of the series show the modal conditions of the plus selected and of the minus selected races respectively.

set from a common stock. In the course of the selection they had become very different in appearance, the plus race being practically black all over as seen from above, the minus race white all over except for a black hood on head and shoulders. In classifying the young of each generation of rats an arbitrary set of grades was found useful. (See fig. 1.)

In order to compare the genetic value of the gene proper for the hooded character in one of these races with its value in the other, it was necessary first to eliminate all modifying genes or else to make them similar in the two races. To do this the plan was adopted of making repeated crosses of each race with a third race, entirely free from the hooded character, thus combining with the residual heredity of the third race the hooded character from each of the selected races. A race of wild rats was chosen as the third race and tables 1 and 2 show how crosses with this race affected the grade of the hooded character as recovered in hooded individuals in the F_2 generation.

A first cross of the plus race (table 1) lowered the grade of the hooded character from about +3.73 to +3.17. A second cross brought a slight rise in the mean grade of the extracted hooded young to +3.34, and a small group of 19 hooded young extracted from a third cross had a mean grade of +3.04. It will be observed that the hooded character was lowered not over three-fourths of a grade by three successive crosses. This fact led me to conclude provisionally in 1916[4] that the hooded gene proper had really changed in the course of our selection experiments, since after the crosses it *remained different* from what it had been originally. This view is obviously erroneous in the light of the results obtained from the minus crosses subsequently studied.

TABLE 1

RESULTS OF CROSSING THE PLUS SELECTED RACE WITH A WILD RACE

	MEAN GRADE	STANDARD DEVIATION	NUMBER OF HOODED YOUNG
Control, uncrossed plus race, generation 10	+3.73	0.36	776
Once extracted hooded F_2 young	+3.17	0.73	73
Twice extracted hooded F_2 young	+3.34	0.50	256
Thrice extracted hooded F_2 young	+3.04	0.64	19

TABLE 2

RESULTS OF CROSSING THE MINUS SELECTED RACE WITH A WILD RACE

	MEAN GRADE	STANDARD DEVIATION	NUMBER ON HOODED YOUNG
Control, uncrossed minus race, generation 16	−2.63	0.27	1,980
Once extracted hooded F_2 young	−0.38	1.25	121
Twice extracted hooded F_2 young	+1.01	0.92	49
Thrice extracted hooded F_2 young	+2.55	0.66	104

The crosses of the minus selected race were started some six generations later in the history of our selection experiments than were those with the plus selected race. They gave results much more striking than those of the plus crosses. (See table 2.) The mean grade of the minus race, when the crosses were started, was −2.63. The F_2 hooded young from a first cross with the wild race were of mean grade −.38, a change of over two grades. A second cross produced hooded F_2 young chiefly *plus* in character, mean grade +1.01. A third cross produced F_2 hooded young exclusively plus in character, mean +2.55. One family in this lot of thrice extracted hooded young, consisted of 14 hooded individuals of mean grade +3.05, almost exactly identical in mean grade with the thrice extracted hooded young of the plus series (table 1).

This result indicates that three crosses with a third race had sufficed practically to eliminate whatever differences had been produced in the minus and

plus races respectively by long continued selection in opposite directions. Those differences accordingly were based on residual heredity, not on changes in the hooded gene proper. For when the residual heredity was equalized, the hooded character appeared substantially the same in the two races. These findings harmonize with the idea that the residual heredity in question consists of several modifying genes independent of the hooded gene proper. Another point favoring that interpretation is the increased variability of the hooded character following the first cross, and its subsequent decrease following the second and third crosses. See the column, standard deviation, in tables 1 and 2.

These results favor the widely accepted view that the single gene is not subject to fluctuating variability, but is stable like a chemical compound of definite composition and changes only similarly, by definite steps (mutation in the sense of Morgan, not of DeVries). They offer no obstacles to the proposition of Johannsen (ably supported by East), that a gene terminology is adequate to express all known varieties of inheritance phenomena.

The full results of this investigation will be published by the Carnegie Institution of Washington.

[1] Bateson, W., *Report I to the Evolution Committee of the Royal Society*, 1902, p. 12.
[2] Castle, W. E., and Phillips, J. C., *Carnegie Inst. Washington, Pub.*, No. 195, 1914.
[3] Johannsen, W., *Elemente der exakten Erblichkeitslehre*, 1909.
[4] Castle, W. E., and Wright, S., *Carnegie Inst. Washington, Pub.* No. 241, 1916.

BUD VARIATION

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The common experience of horticulturists and plant breeders is that propagation by buds, cuttings, layering, etc. (asexual propagation) yields a comparatively uniform progeny, while propagation by seed (sexual reproduction) and especially that which involves mating of unlike parents whether of the same or of different species or races, is likely to give decided variation among progeny. On the other hand, common experience and practice recognizes the widespread occurrence of bud variations and the importance of utilizing them in developing new types of important commercial races, or in maintaining old races at a high standard, as is well illustrated by the recent studies (Shamel and others 1918) of bud variations in the citrus fruits.

In scientific and theoretical breeding, much attention has been given to the study of heredity in sexual reproduction. In many species this is the only method that can be utilized, and a knowledge of such heredity is of great practical as well as of theoretical interest. When, however, the question arises re-

garding the constancy of characters or of assumed factors of heredity, it seems very evident that critical studies of somatic variations, especially wherever it is possible to propagate vegetatively, are of fundamental importance.

To Darwin, bud variations in plants were evidences of the very indiscriminate variability that is everywhere present in organisms. Their broad significance and range were recognized by his conclusions that they include: (1) reversions to remote ancestral characters; (2) reversions (in hybrids) to the more immediate parental qualities; and (3) cases of real spontaneous change in hereditary composition of continuous as well as of discontinuous range. Darwin did not believe in fixed hereditary units.

These same types of bud variation are, in general, recognized by de Vries (1901). He attempts, however, to assign mutational value of discontinuous rank to the spontaneous somatic variations quite as he does to seed mutations. Yet he recognizes a wide variability and irregular hereditary performance in both. For example, he describes half races, middle races and eversporting varieties in the various steps in the development of varieties from pure species involving characters frequently concerned in bud sports and ascribes the series of changes to conditions of latency, semilatency, lability or activity of hereditary units (pangens). To many critics of the mutational doctrines it is difficult to recognize such spontaneous hereditary variations as discontinuous either from the facts or explanations presented by de Vries or by other investigators. We may note further that many bud variations, such as the development of variegated branches on pure green stems were considered by de Vries as progressive mutations.

In general, Cramer's (1907) classification of bud variations follows that of de Vries for seed mutants with, however, a greater emphasis on the operation of Mendelian segregations in certain groups. He recognizes, however, quite as did Darwin and de Vries, the occurrence of a large group of bud variations in which continuous and sporadic or eversporting variability is in evidence.

The present day Mendelian studies of the seed progenies from bud variations and of characters exhibiting such variations show as a rule decidedly mixed and non-Mendelian results, or, at least, their interpretations involve subsidiary hypotheses. Some special tendencies in such interpretations may be noted: (1) the assumption that the transmission of certain characters is by the cytoplasm rather than by the nucleus; (2) the assumption that somatic variations are losses of hereditary factors accomplished by qualitative or segregative cell divisions, and (3) the claim that hereditary factors may themselves sporadically change, and the new factors come to immediate expression by dominance, or remain recessive, or exhibit various influence as modifying factors. Thus in certain attempts to analyze the heredity of seed colors in variegated corn it is assumed that factors for variegated color can change reciprocally in a series of somatic divisions and that as many as ten 'multiple allelomorphs' may be present, which, as Jennings (1917) remarks, "leap back and forth from one character to another in bewildering fashion."

A better understanding of the nature of the tissue complex in certain bud variations has been gained from the knowledge of chimeral structures. When a somewhat permanent somatic variation occurs in only a part of the cells or in a single cell of a growing point such a cell or cells may be so situated that the cell progeny form permanent layers giving periclinal chimeras, or sectors giving sectorial chimeras. There is also the possibility that irregular processes of development or the occurrence of repeated somatic variations during organogenesis may give complex mixtures or hyperchimeras. Anatomical proof of the existence of such chimeras was first presented by Baur (1909) and the experimental production or interspecific chimeras was demonstrated by Winkler (1907).

Numerous cases of albomarginate variegation are apparently of the periclinal type. The originial variation in such cases is partial, affecting a part of a growing point only. Further changes, such as return to pure green branches, may involve simply a mechanical readjustment of the elements present in the growing points (Stout 1913). Chimeral association of cells differing sporadically but more or less permanently in fundamental hereditary qualities undoubtedly accounts for much of the irregularity seen in the seed progeny of bud sports. Various types of chimeras especially periclinal and hyperchimeras, without doubt grade imperceptibly into cases of ordinary differentiation in which the cells quite alike in fundamental hereditary qualities become differentiated through their relations as parts of the whole.

In general, our available knowledge regarding somatic variations indicates that they show a wide range of variability suggesting that hereditary elements or units are themselves variable even in a series of somatic cell-divisions. The evidence is especially convincing, for here there is a most direct lineage of cell elements far more simple than that obtained in reproduction by seed progeny which involves the intricacies of periodic reduction and fertilization. Unquestionably the phenomena of bud variation involve the most fundamental questions of heredity. The intensive study of bud variants in successive generations propagated vegetatively should reveal definite facts regarding the nature, frequency, and permanence of spontaneous changes. Since 1911 the writer has studied bud variations in a variety of the variegated *Coleus* with these aims in mind. Over 1211 pedigreed plants have been grown, comprising fourteen generations (two each year), all propagated by cuttings, the first of which were taken from two similar sister plants.

The frequent variations that have appeared range from sudden changes to gradual fluctuations, and these may first become evident in a part (even a small area) or the whole of either a leaf, a bud, or a plant. The characters studied have been those of leaf form and leaf coloration.

The somatic variations found in leaf coloration involved (1) gain or loss, increase and decrease of green and yellow, (2) reversals of the relative positions of the green and yellow in leaves, (3) increase and decrease of red pigmentation, and (4) changes in the distribution of the red pigmentation, especially tha

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giving concentration in the epidermis of the upper surface of the leaves. Some of the variations involve very striking changes in epidermal pigmentation, superficially resembling chimeral relationships. During the first seven generations, sixteen distinct color patterns were obtained by bud variation and isolated by selection; fifteen of these were produced as marked sudden variations, and six of the types also occurred as fluctuating variations. One pattern has appeared only as a fluctuation. Between any of these types a wide range of intermediates was found from which many additional patterns might probably have been isolated. There has been reversion to parent patterns; colors that have been lost or thrown out have reappeared; yellow-green patterns have given pure green sports and later the yellow has reappeared.

A calculation of the frequency of bud variations on the basis of the estimated number of buds that developed into branches shows clearly that decrease of red occurred with about twice the frequency as did increase of red; likewise decrease of yellow occurred about twice as often as increase of yellow. Among sister lines of clonal descent there were marked differences in the ratios of frequency for any one change in coloration. The most frequent change was loss of yellow with increase of green, for which the frequency ratio was 1:2960. The change occurring with least frequency was that of increase of epidermal red pigmentation to solid red for which the ratio was 1:19,250.

Variations in leaf form were fully as striking as those of pigmentation. Deeply laciniate-leaved forms arose in thirteen instances as fluctuations affecting an entire plant, and in one case as a decided bud variation. A striking feature of the laciniate character was the marked periodicity in its development; plants of the variety having strongly laciniate leaves in winter produced entire leaves in summer, while the great bulk of the sister plants of other varieties produced only entire leaves. In general these variations in form are continuous and the extremes are in decided contrast with each other.

Selection for extremes and for intermediates has in every case given a progeny of marked constancy but with further fluctuations and sporadic variations about a new mode. The types thus arising are for purposes of propagation the equivalents of the 'Kleinarten' or 'biotypes' that commonly occur in species propagated by seed. In their bearing on the theories of continuous variation and the effects of selection, my results are quite identical with those obtained by Castle and Phillips (1914) in their study of color patterns in biparental reproduction in rats and interpreted as indicative of actual variation in the hereditary units. The results are also quite identical with those Jennings (1916) has obtained with *Difflugia*, by asexual propagation analogous to that I have used in *Coleus*.

It is quite clear that the changes seen in *Coleus* do not involve a permanent loss of definite hereditary units by vegetative segregation. There is also no opportunity for any such recombination of multiple modifying factors as is assumed to give similar variations in sexually reproduced progeny. As far as is known vegetative propagation gives the greatest possible degree of purity

in cell lineage uncontaminated by the recombinations involved in the reduction and fusion accompanying sexual reproduction. The evidence is hence very conclusive that the hereditary complex and that individual units of the complex are subject to variations that become manifest either as sudden mutations or as fluctuating variations, and that any of these may perpetuate themselves.

The facts suggest strongly that the possibilities for the development of red, green and yellow may be present in all cells as metidentical characters (in the sense used by Detto, 1907). The total production, the distribution, and the concentration of the various chemical substances concerned, however, plainly involve interactions between different cells or groups of cells and are in this sense epigenetic. The explanation suggested by the production of patterns in colloids by the Liesegang precipitation phenomena, especially as applied by Gebhardt (1912) to the markings of butterfly wings and by Kuster (1912, 1917) to the development of many types of variegation in plants including *Coleus*, seems to apply to the production of color patterns in *Coleus*. On this view colored patterns may be considered as due to the formation of localized centers for the development, diffusion and concentration of pigments.

In *Coleus* both the (1) fundamental qualities (metidentical) and the (2) processes of cellular and tissue interaction immediately involved in the development of patterns exhibit spontaneous changes that are continuous in degree and are quite constant from the first or can be made so by selection.

Colored illustrations of the principal color patterns obtained, together with the presentation of data (for the first four years of the study) have already been presented (Stout 1915). With the facts and conclusions there given, the results since obtained are fully in agreement.

Baur, E., *Zs. Ind. Abs. Vererbs.*, **1**, 1909, (330–351).

Castle, W. E., and Phillips, J. C., *Piebald rats and selection*, 1914.

Cramer, P. J. S., *Kritische Uebersicht der bekannten Falle von Knospenvariation*, 1907.

Detto, C., *Biol. Centralb.*, **27**, 1907, (80–95, 106–112, 142–160, 162–173).

Gebhardt, F. A. M. W., *Verh. Deuts. Zool. Ges.*, **22**, 1912, (179–204).

Jennings, H. S., *Genetics*, **1**, 1916, (407–534); *Amer. Nat., Lancaster*, **51**, 1917, (301–306).

Küster, E., *Beiträge zur entwicklungs mechanischen Anatomie der Pflanzen*, 1913; *Flora*, **10**, 1917, (1–33).

Shamel, A. D., Scott, L. B., and Pomeroy, C. S., *Washington U. S. Dept. Agric. Bull.*, 1918, Nos. 623, 624, 697.

Stout, A. B., *Bull. Torrey Bot. Club*, **40**, 1913, (367–372); *Carnegie Inst., Washington*, 1915, *Pub.* No. 218.

de Vries, H., *Die Mutationstheorie*, 1901.

Winkler, H., *Ber. Deuts. Bot. Ges.*, **25**, 1907, (568–576).

THE GROWTH RATE OF AN ANNUAL PLANT HELIANTHUS*

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Communicated by R. Pearl, February 28, 1919

If we assume that growth is a dynamic process and that the organism is produced as its end-product, certain relations ought to exist between the size of the organism at any given time and the final size attained in time, T.

Growth begins at a slow rate, but as the reaction proceeds it goes on at an increasingly rapid rate until it reaches a maximum velocity, then the rate decreases until the reaction comes to a stop. This is precisely what happens in autocatalytic processes in which the reaction is catalyzed by one of its own products. It therefore becomes of interest to inquire whether the growth rate of an organism, or group of organisms, approximates the rate of autocatalysis. As will be shown in this article, the equation of autocatalysis expresses admirably the growth rate of plants studied.

Growth may be considered as a function of two variables. The first of these is the genetic constitution of the individual. The second is the resultant of all those factors that make up what is commonly called the environment of the organism. The factors of the first group are essentially *internal*; those of the second group, essentially *external*. In analyzing the growth process it is of interest to separate so far as possible the results of these two classes of factors. If the growth rate follows approximately the course of an autocatalytic reaction, it is safe to assume that it is controlled by some internal factor resident in the organism. If it departs from the theoretical course more widely and uniformly than might be expected upon the basis of pure chance, we may believe that some other, presumably external, factor is of sufficient weight to control or, at least, influence the growth rate.

The studies embodied in the present paper are based on measurements of a group of fifty-eight sunflowers, grown for the purpose on the grounds of the Citrus Experiment Station, Riverside, California. They were grown on a small piece of tolerably uniform soil to which water sufficient to maintain satisfactory soil-moisture conditions was applied every seven days. The plants grew from the middle of May to the middle of August during a time when heat and light were ample for plant growth. As soon as the plants had reached an average height of more than 10 centimeters, sixty of the normal, appearing plants were selected at random throughout the small plot and marked with suitable labels. (During the course of the observations, two plants had to be eliminated on account of accidents). Each plant was marked with india ink at a distance of 10 centimeters below the growing tip. This mark served as a point from which further measurements were made. The

sunflower was chosen for this work because of the fact that it grows without producing branches and it was thought that measurements of growth and weight represented the growth of the entire organism with a fair degree of accuracy. The adjacent plants were removed from the vicinity of those selected so that there was space of about 20 centimeters between any plant and its nearest neighbor. In short, environmental conditions were made as nearly uniform for the individuals in this small group as it was feasible to make them under field conditions. In the latter part of July the terminal buds began to develop into blossoms and coincidentally the plants ceased to elongate.

The plants used in these studies were evidently of mixed ancestry as shown by the presence of branched and unbranched individuals. The seed had been bought at a seedstore and nothing was known of its pedigree. The branching habit is regarded by Shull (1908) to be a Mendelian character.

TABLE 1

CONSTANTS FOR GROWTH AND VARIATION IN HEIGHT OF HELIANTHUS PLANTS

DAYS	MEAN HEIGHT	INCREASE OF MEAN HEIGHT	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
	cm.	*cm.*		
7	17.93 ± 0.14	7.93 ± 0.14	1.62 ± 1.01	9.03 ± 0.56
14	36.36 ± 0.43	18.43 ± 0.43	4.83 ± 0.30	13.28 ± 0.85
21	67.76 ± 0.78	31.40 ± 0.89	8.93 ± 0.56	13.17 ± 0.84
28	98.10 ± 1.38	30.34 ± 1.59	15.60 ± 0.98	15.90 ± 1.02
35	131.00 ± 1.73	32.90 ± 2.21	19.52 ± 1.22	14.90 ± 0.95
42	169.50 ± 2.21	38.50 ± 2.81	25.00 ± 1.56	14.75 ± 0.94
49	205.50 ± 2.92	36.00 ± 3.66	33.00 ± 2.07	16.06 ± 1.03
56	228.30 ± 3.41	22.80 ± 4.49	38.47 ± 2.41	16.84 ± 1.08
63	247.10 ± 3.80	18.80 ± 5.10	42.92 ± 2.69	17.38 ± 1.12
70	250.50 ± 3.76	3.40 ± 5.35	42.48 ± 2.66	16.95 ± 1.09
77	253.80 ± 3.99	3.30 ± 5.48	45.06 ± 2.82	17.75 ± 1.13
84	254.50 ± 3.89	0.70 ± 5.57	43.90 ± 2.75	17.25 ± 1.11

One important difference should be noted between the plants described by Shull and those in our series, viz: Shull's plants branched from the lower nodes of the stalk, while ours branched only from the upper nodes. Church (1915) regards the branched form as a mutant of the unbranched and believes that it is the oldest mutation on record.

The branched form usually produces a head on the apex of each branch, whereas the unbranched form produces one head from the apical bud of the stem and no other.

This mixture of branched and unbranched stems is not thought to affect the validity of the measurements upon which the present study is based, since only seventeen out of the fifty-eight plants were branched. The average heights of the two classes at maturity were close enough together to be within the range of the probable error, though the length of the average growing season of the branched plants was 4.6 days longer than that of the

unbranched plants. The number of heads produced by the branched plants ranged from three to thirteen.

Rate and Extent of Growth.—Fifty-eight plants were measured at seven-day intervals, from the time when each plant was marked 10 centimeters below the growing tip until no further elongation occurred. On the eighty-fourth day, when the last measurement was taken, the plants averaged 254.5 centimeters high to the upper side of the head, with a range from 164 centimeters to 339 centimeters. The mean growing period in days was 69.79 ± 2.17. The mean height of the plants is shown by figures in table 1, along with the standard deviation and coefficients of variability. The mean height of plants at seven-day intervals is shown graphically in figure 1.

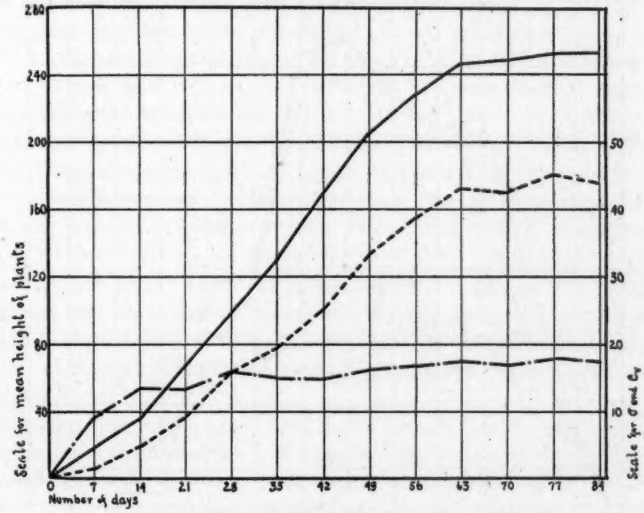

FIG. 1. GROWTH AND VARIABILITY OF HELIANTHUS

Mean height of plants ————————
Standard deviation — — — — — — — —
Coefficient of variability —— - —— - —— -

The data show that the plants rapidly increased in height, the maximum growth rate being exhibited between the thirty-fifth and the forty-second days, i.e., about the middle of the grand period of growth. The growth rate was smaller at the start, rapidly increasing until it reached its maximum and then declining as it approached the end of the grand period of growth.

The standard deviations of the mean values increase as the means increase but not at a proportional rate. In this case the coefficient of variability is a better measure of the variability since its size is more nearly independent of the height of the plants. This coefficient does not increase during the latter

part of the growth period. It increased very rapidly at first, but remained fairly constant after the 28th day. The variability thus appeared to reach a constant value which changed but slightly as the plants approached maturity.

The decline in the growth rate of a plant began to appear as the flower bud on the apex of the stalk began to be differentiated. As the 'head' developed, the growth of the stalk became slower, showing agreement with the condition accompanying tassel formation which Pearl and Surface (1915) found in maize. After the flowers of the composite 'head' had been pollinated there was no fur-

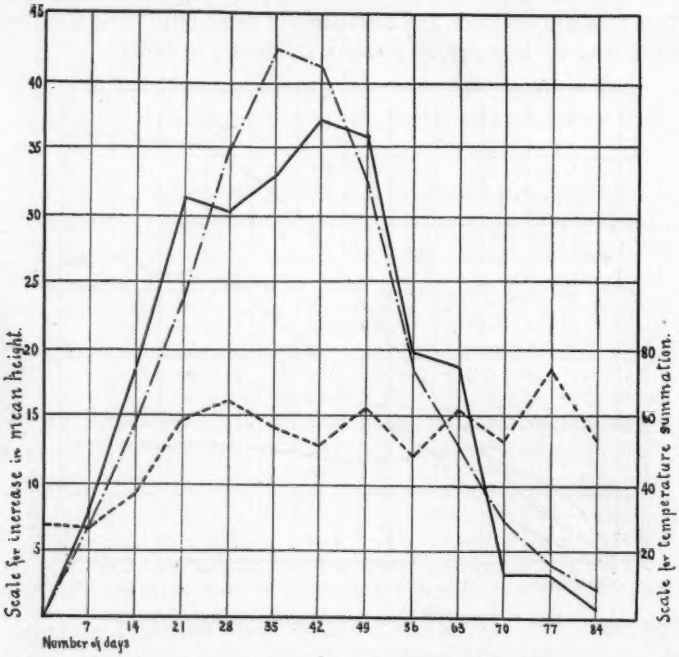

FIG. 2. INCREASES IN MEAN HEIGHT OF HELIANTHUS AT 7 DAY INTERVALS

Observed mean height ————————
Theoretical mean height ——·——·——·—
Temperature summations — — — — — — — —

ther elongation of the stalk. It is evident that from this time on the growth forces of the plant are devoted to seed-formation instead of stalk-elongation. Thus, variability in the time of blossoming may, and undoubtedly does, influence the grand period of growth and the total growth of this plant.

When the flowers have been pollinated the head which previously stood erect becomes pendant. The floral surface which is uppermost during the prepollination period, is lowermost in the post-pollination period.

An examination of the consecutive increases in mean height of the plants may help to give a clearer picture of the distribution of the growth increments of these plants. The mean growth increases observed at seven-day intervals have been plotted out in figure 2. The increases, starting from the day on which the plants were marked, show a general trend upward for the first forty-two days and a decline for the following forty-two days. Inspection of the graph shows that the line does not rise and fall smoothly, there being several abrupt changes. The mean height increased rapidly from the beginning to the twenty-first day. The rate fell off somewhat to the twenty-eighth day, then increased gradually until the maximum was reached on the forty-second day. From the forty-second to the forty-ninth day the rate fell off slightly and then declined abruptly to the fifty-sixth day. From the fifty-sixth to the sixty-third day there was only a slight decline in the rate, but from the sixty-third to the seventieth day there was a rapid decline followed by a halt until the seventy-seventh day, and then a descent to a point near the eighty-fourth day where growth ceased entirely.

The Correspondence Between Growth and Autocatalysis.—It may next be in order to inquire concerning the nature and action of some of the internal factors which influenced the growth of these plants. Studies on the growth of animals made by Robertson (1908, 1915) and of bacterial activity made by Miyake (1916) have shown the similarity of these processes to that of autocatalysis. In autocatalysis one of the products of the reaction catalyzes the reaction. Such reactions begin slowly, but as more of the catalyzing substance is produced the reaction goes on at an increasingly rapid rate. As the supply of reacting substances is used up, the reaction begins to slow down and comes eventually to a stop.

Brief mention will be made here to the formula used to express the course of an autocatalytic reaction. The reader who wishes more complete mathematical discussion should consult papers of Robertson (1915) and Miyake (1916). An autocatalytic reaction may be expressed by the differential equation

$$\frac{dx}{dt} = Kx\,(A - x),$$

in which A is the initial quantity of material subject to transformation, x is the amount transformed at time t, and K is a constant. The integral form of this equation is

$$\log \frac{x}{A - x} = K\,(t - t_1),$$

in which t_1 is the time at which the reaction has run half way to equilibrum; that is, the time at which $x = A/2$.

Translating these functions into terms of growth, we let A represent the final mass of the plant; x, the size of the plant at any time, t; t_1, the time at which

the mass of the plant is half the final mass, etc. Obviously it would be better to weigh the sunflower plants, but as this would require severance between the plant and the soil, it would not have been practicable to use the same plants for subsequent measurements. In the case of a straight unbranched stalk (such as most of these sunflowers were), it seems sufficiently accurate to use the height of the plant as an index of the amount of growth, at least up to the time of flowering.

In the case of these sunflowers, A is 254.5 cm., t_1 is 34.2 days, then

$$\log \frac{x}{254.5 - x} = K\ (t - 34.2).$$

Substitution of the various values of x and corresponding values of t gives the corresponding values of K which are shown in the third column of table 2.

TABLE 2

CONSTANTS FOR THE MEAN HEIGHT OF SUNFLOWERS AT SUCCESSIVE INTERVALS

t	X (OBSERVED)	K	X (CALCULATED)	θ
days	*cm.*		*cm.*	*cm.*
7	17.93	0.04128	17.05	−0.88
14	36.36	0.03851	31.43	−4.93
21	67.76	0.03341	55.35	−12.41
28	98.10	0.03274	90.09	−8.01
35	131.00	0.03250	132.21	+1.21
42	169.00	0.03794	173.06	+4.06
49	205.50	0.04196	205.64	+0.14
56	228.30	0.04312	227.01	−1.29
63	247.10	0.05295	239.74	−7.36
70	250.50	0.04997	246.87	−3.63
77	253.80	0.05892	250.56	−3.24
84	254.50	—	252.46	−2.04

The average value of K determined in this way is .0421. Using this value of K we proceed to find the values of $K\ (t - t_1)$, and from these, with the assistance of Robertson's tables, a series of calculated values of x were obtained. These were the theoretical heights of the plants at the successive intervals provided the orginial equation was a correct expression of the growth rate. The divergence, θ, between the observed and the theoretical values is shown for each interval in the last column of the table. On the whole, the correspondence between the observed and the theoretical values is very satisfactory. The observed and calculated heights of the plants are shown graphically in figure 3.

More accurate comparison of these values was made by testing the goodness of fit of the theoretical to the observed curve. Employing the method given by Elderton (1902), it was found that $P = .9256$, which is taken to indicate a satisfactory fit, since in approximately ninety-two cases out of one

hundred, a random sampling would give values diverging more widely from the theoretical than those actually found.

Since the observed values agree so well with the theoretical values, it seems safe to assume that the growth rate is governed by constant internal forces rather than by external forces which would be expected to be more casual in-operation.

The theoretical values for the consecutive increases in the mean height of the plants give a smoother curve than the observed values give, as shown in figure 2. The sag in the observed curve near the twenty-eighth day does not appear in the theoretical curve. The summit of the theoretical curve is near

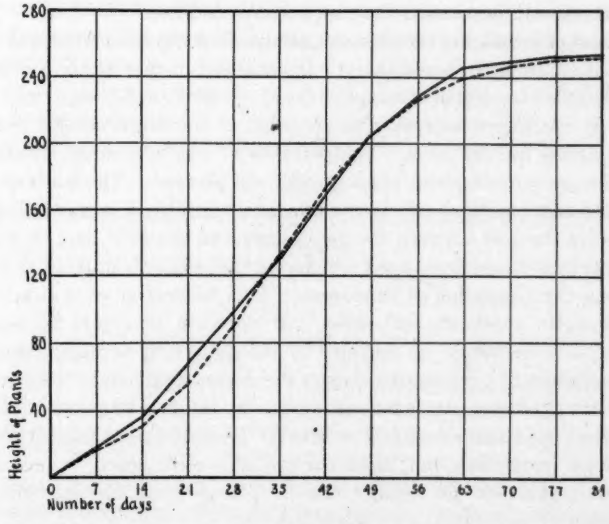

FIG. 3. COMPARISON OF OBSERVED AND CALCULATED VALUES FOR THE MEAN HEIGHT OF HELIANTHUS

Observed ————————

Calculated — — — — — — — —

the thirty-fifth day, thus agreeing with the computed value of $t_1 = 34.2$ days, the time at which half the final height is attained and at which growth is most rapid.

The assumption having been made that the growth was more largely governed by internal than external factors, and positive evidence in favor of the assumption having been obtained, it is next in order to investigate the relationship between growth and some of the more prominent factors of the external environment.

Temperature is known to have a potent effect upon growth, especially if it departs widely from the optimum requirements of the organism. In a prob-

lem like the present, we are more concerned with the temperature summation than with the mean temperature unless the range is very large.

It is clear that we shall not arrive at a correct value if we take an arithmetical average of the maximum and minimum daily temperatures, because we do not in that way take any account of the time during which either prevailed, or of the range of temperatures. For example, the minimum temperature on a given day may be 50° and the maximum temperature 90°, an average of 70° but if the maximum temperature prevails for only two hours out of the twenty-four, while the temperature varies between 50° and 65° for most of the daily period, it is obvious that the mere arithmetical mean, 70°, is a false expression of the temperature. The values must be weighted in order to give an average which correctly represents the temperature condition.

A method of measuring temperature summations has been employed which is believed to be fairly satisfactory. It consisted in finding the product of hours multiplied by degree of temperature above 40°F. and is expressed in degree-hours. A degree-hour may be regarded as one degree of effective temperature acting for one hour. The point 40°F. was arbitrarily chosen as a basal point, at or near which plant growth will proceed. The method of obtaining the summation of effective temperature consisted in measuring with a planimeter the area between the pen tracing and the 40°F. line on thermograph records obtained from a self registering thermograph situated about 100 yards from the plantation of sunflowers. This method gives a direct index of temperatures above the 40° point, but does not take into account the efficiency of temperatures as assumed by the van't Hoff-Arrhenius principle.

The coefficient of correlation between the degree-hours and the increase in height of the sunflower plants for each seven-day interval was calculated. Its value turned out to be $r = 0.199 \pm 0.187$. There are some indications here of a positive correlation, but, since the probable error nearly equals the coefficient in magnitude, no reliance can be placed upon the existence of a correlation.

Reference to the graph showing temperature summations in figure 2, shows little correspondence with the curve representing growth increases, except in the first twenty-one days of the period.

In a somewhat similar way we have investigated the possibility of a correlation between growth rate and the coefficient of the evaporating power of the air, the latter value being obtained from the readings of a spherical porous-clay atmometer-bulb located about one hundred yards from the plants. The coefficient of correlation for these values was even less than that in the foregoing case, being 0.041 ± 0.202. The coefficient in itself is so small as to lack significance, and when compared with its probable error it fails entirely to indicate any correlation between these two factors.

These statements are not to be construed as arguments against the effect of temperature and transpiration upon the rate of growth of plants. Our argument is merely intended to emphasize the greater importance of the inter-

nal factors in determining the growth, reproduction and senescence of the plant, factors which are so potent that they overbalance external factors so long as the latter do not too closely approach minimum or maximum values.

That the oncoming of reproductive processes induces changes in the growth rate of the organism is a fact too well known to require comment, but is well illustrated by the behavior of the sunflower.

It appears that growth, its rate, its grand period, and, to some extent, its amount are so steadily controlled by factors inherent in the genetic constitution of the sunflower that these factors are prepotent unless the external conditions depart widely or repeatedly from the optimum. Plants in this respect are more sensitive to variations in their external environment than animals, yet these studies show that even plants are not entirely dependent upon environmental (external) conditions for determining their growth rate.

It may be of interest to inquire whether the formula of autocatalysis applies, as well to the smaller plants as to the medium and large plants of this group and how the mean values of K for different groups agree.

TABLE 3

HEIGHT AND GROWTH CONSTANTS OF PLANTS ENDING IN THEIR GROWTH IN DIFFERENT QUARTILES

	QUARTILE			
	I	II	III	IV
Final height of plants.....	198 cm.	238 cm.	272 cm.	312 cm.
Mean value of K.....	0.0440±0.0011	0.0421±0.0016	0.0429±0.0017	0.0443±0.0023
Standard deviation of mean value of K.....	0.0052±0.0008	0.0079±0.0011	0.0079±0.0012	0.0111±0.0016

As a basis of classification we divided the plants into quartiles, based upon their heights at maturity. Quartile I, contained the smallest plants, quartile II, the next larger and so on. Since 58 is not exactly divisible by 4, the quartiles were not exactly of equal size: quartiles I and III contained 15 plants each and quartiles II and IV contained 14 each. An average of the heights of each group of plants at each time interval, t, gave a corresponding value of x, from which the several values of K were computed. (See table 3).

The mean values of K are remarkably constant for the different quartiles, in fact all are within the range of their probable errors. This may be regarded as evidence that the growth constant has the same value for all classes of plants in this population without regard to their relative heights, since the relation between the final height and the height at any given time obeys the same principle.

A brief consideration of a parallel case will make it evident that such a relation must exist in this sort of reaction. The inversion of cane sugar is a familiar case of autocatalysis in which one of the products catalyzes the reaction.

It is plain that the amounts of invert sugar finally formed in four different flasks may vary, depending upon the amount of cane sugar originally present, yet the constant of autocatalysis remains the same and the time may be the same in each case. This relation exists because the quantity dx/dt is proportional to the quantity of cane sugar remaining, which may be represented by $(a - x)$ where a is the original quantity of cane sugar at the beginning, i.e., when $t = 0$.

The senior author has discussed the distribution of these plants in the several quartiles in a paper soon to be published (Reed, 1919), showing that said distribution is due to some agency operating to cause variability in height other than purely casual agencies which might be expected upon the basis of pure chance. The data presented in table 3, indicate that no difference in the growth constants exists which can account for the larger or smaller size of a part of the population. Whether the differences in the amount of material produced, i.e., the size of the plants, is to be referred to differences in amount or activity of the catalyst, or of the substrate, cannot be discussed upon the basis of the data now in hand.

An additional point may be discussed in this connection, viz., "Are the values of the growth constants more widely dispersed from their means in one quartile than in another?" We may take the standard deviations of the means as a measure of the dispersion of the individual values. Reference to table 3 shows that the standard deviations increase from the lower to the upper quartiles, which would seem to indicate that the growth rate of the larger plants fluctuates more from the mean than is the case in the smaller plants.

Summary.—1. Measurements of sunflower plants at intervals of seven days showed that their growth rate approximated closely the course of an autocatalytic reaction.

2. The close correspondence of the actual mean height of plants to that required by the equation of autocatalysis is taken to indicate that the growth rate is governed by constant internal factors rather than by external factors which would be expected to be more casual in their influence.

3. The growth rate showed no strong correlation either with temperature-summations, or with transpiration-summations.

4. The value of the growth constant was not perceptibly different for the larger or smaller plants in this population.

*Paper 56 from the University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

Church, A. H., *quoted* in Cockerell, T. D. A., *Amer. Nat., Lancaster*, **49**, 1915, (609).

Elderton, W. P., *Biometrika, London*, **1**, 1902, (153–163).

Miyake, K., *Soil Science*, **2**, 1916, (481–492).

Pearl, R., and Surface, F. M., *Zs. indukt. Abstam.- Vererbungslehre*, **14**, 1915, (97–203).

Reed, H. S., (1919), *Amer. J. Bot.*, (in press).

Roberston, T. B., *Arch. Entwicklungsmechanik*, **26**, 1908, (108–118); *Ibid.*, **37**, 1913, (497); *Berkeley, Univ. Cal. Publ. in Physiology*, **4**, 1915, (211–288).

Shull, G. H., *Bot. Gaz., Chicago*, **45**, 1908, (103–116).

ON SOME METALLIC DERIVATIVES OF ETHYL THIOGLYCOLLATE[1]

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Communicated by J. J. Abel, March 10, 1919

In 1910 Abel[2] discovered that thioglycollic ester dissolves antimony trioxide with the greatest ease, forming an antimony derivative, $Sb(SCH_2CO_2C_2H_5)_3$, according to the equation: $2Sb_2O_3+6HSCH_2CO_2C_2H_5=2Sb(SCH_2CO_2C_2H_5)_3+3H_2O$. The antimony compound separates as a heavy oil which, when treated in absolute alcohol with ammonia, yields the corresponding amide, $Sb(SCH_2CONH_2)_3$, obtained by precipitation from alcohol with ether as a colorless or slightly reddish, semiresinous mass soluble in water in all proportions with neutral reaction. The experiments of Rowntree, carried out in collaboration with Abel, showed that the new amide is a very powerful trypanosomicidal substance.

Professor Abel found that the thioglycollic ester reacts energetically with mercuric oxide also, and in order to determine whether the reaction discovered by him is of general applicability, he suggested to the writer that he try the action of various other metallic oxides on the ester. It was hoped that the resulting products might be so slightly soluble as not to be toxic when applied on open wound surfaces, but yet soluble enough to be antiseptic and bactericidal. Abel's expectation that his reaction would prove to be general has been confirmed; whether the products formed are of pharmacological and therapeutic value we have not yet had an opportunity to determine.

Following Abel's general method (for details see the forthcoming paper in the Journal of the American Chemical Society), the compounds listed below have been prepared and analyzed.

Triethyl bismuthtrithioglycollate, $Bi(SCH_2CO_2C_2H_5)_3$

Diethyl mercurydithioglycollate, $Hg(SCH_2CO_2C_2H_5)_2$

Ethyl silverthioglycollate, $AgSCH_2CO_2C_2H_5$.

A copper compound with 9.3 % of copper for which no simple formula can be derived; the normal compound, $Cu(SCH_2CO_2C_2H_5)_2$, would contain 21.06% of copper.

Zinc, arsenic, and tin compounds were also prepared but have not yet been analyzed.

[1] A more detailed report of this investigation will appear in the May issue of the Journal of the American Chemical Society.

[2] Rowntree, L. G., and Abel, J. J., *J. Pharmacology Exper. Therapeutics*, 2, 1910, (108).

AN ANALYSIS OF THE RELATION BETWEEN THE TEMPERATURE AND THE DURATION OF A BIOLOGICAL PROCESS

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Communicated by J. Loeb, February 17, 1919

1. Biological processes exhibit variations in rate at different temperatures. The speed of a given activity increases with an increase in the temperature, usually in the form of an exponential function, occasionally in a linear manner. At higher temperatures, however, the rate of increase falls off. The velocity of the process reaches a maximum at a critical temperature, above which the activity declines rapidly or ceases entirely.

Such vital processes are undoubtedly conditioned by chemical and physical reactions. It should therefore be possible to analyze these variations in terms of the changes usually associated with the relation between chemical and physical reactions and the temperatures at which they occur. This has been difficult to accomplish except in the most general terms. The variations at higher temperatures are attributed to the destructive effect of heat on protoplasm, etc., but no really quantitative analysis of such variations is attempted. It has, however, been possible to accomplish this in a study of the photic sensitivity of *Mya arenaria*.

2. The mollusc *Mya* responds to illumination by a rapid retraction of its siphons. Its reaction time is composed of two parts. The first is a sensitization period during which the animal must be exposed to light in order to respond at the end of the usual reaction time. The second is a latent period during which *Mya* may remain in the dark. At the end of this period the organism responds as if it had been exposed to light for the entire reaction time. The composition of the reaction time is strikingly clear, because the sensitization period is very short,—less than 0.10 second at moderate intensities. The latent period, however, is well above 1.0 second at room temperature.

The sensitization period is conditioned by the velocity of a photochemical reaction. The more intense the stimulating light, the shorter is the time necessary to expose Mya in order to produce a response.

The latent period, however, depends on a reaction, the velocity of which is determined by the amount of substance formed during the exposure to light. The reciprocal of the latent period measures the velocity of its determining reaction. The relation between the velocity and the exposure time is strictly linear for exposures shorter than the sensitization period. Since it is generally true that the velocity of a catalyzed reaction is a linear function of the concentration of catalyst, the latent period is very probably the result of a

chemical reaction which is catalyzed by the substance formed during the exposure to light.

This intimate connection between the two phases of the reaction time makes it possible to investigate the relation between the temperature and the latent period, free from the usual 'rate of heating' and 'time factor' difficulties. By bringing the animal to the desired temperature in the dark, errors resulting from the change of the system during the preliminary and subsequent heatings are largely eliminated. This is because the products of the reaction concerned with the latent period occur only as an immediate result of the exposure to light. They can, therefore, be influenced only after such exposure. The changes which then occur are exactly the ones which it is desired to measure.

The results obtained by determining the latent period at different temperatures, at a constant intensity, will be found in detail in a future number of the Journal of General Physiology. They are, in general, similar to the many that have already been published, with the exception that they are amenable to a clear analysis. With this we shall now be concerned.

3. The relation between the velocity constants (K_1 and K_0) of a chemical reaction at different temperatures (T_1 and T_0), is given by Arrhenius in the following equation:

$$\frac{K_1}{K_0} = e^{\frac{\mu}{2}\left(\frac{T_1-T_0}{T_1T_0}\right)}.$$

The temperatures are absolute, e is the Naperian base, and μ is a constant characteristic of a given chemical reaction. Since only the ratio between the velocity constants is required, there may be substituted in their places the reciprocals of the time required to accomplish a given amount of work.

Using the reciprocals of the latent period at different temperatures in this manner, μ shows a constant value of 19,680 from 13° to 21°C. Between these temperatures the latent period, therefore, varies as if it were conditioned by a single chemical reaction. Above 21°, however, the value of μ decreases steadily until at 31° it is 11,210. This regular decline in the value of μ is equivalent to saying that above 21° the latent period becomes longer than it would be if the process as a whole showed a constant value of μ. At higher temperatures, therefore, the operation of a secondary factor becomes evident. The effect of this is to increase the duration of the reaction concerned fundamentally with the latent period.

4. The steady decrease in the value of μ with rising temperature indicates an increasing effect of the second factor. The results of its operation below 21° are probably not measurable. It should be pointed out that 21°C. is the mean water temperature of the hottest month at Woods Hole.

If we conceive the substance formed during the latent period to be thermolabile, and also that a definite quantity of it is required to cause a response of the animal, the presence of this secondary, modifying factor may be quantitatively determined. At higher temperatures the thermolabile substance is

rendered inactive in appreciable amounts. Consequently the reaction producing the thermolabile substance must proceed longer in order to make up the amount of it required for a response. The interval of time in which all this occurs is very small at temperatures above 21°,—less than one second. The portion of the reaction isotherm which is involved may therefore be considered a straight line. The amount of thermolabile substance formed will thus be a linear function of the time.

By using the original, constant value of μ (=19,680), it is possible to calculate the duration of the latent period at higher temperatures, free from the influence of the additional variable. The differences between the calculated time and the observed time serve as a measure of the effect of the second factor. The difference in time divided by the calculated time gives the percent of the theoretically necessary amount of thermolabile substance which is inactivated at any temperature.

It has been repeatedly shown that the course of inactivation reactions and of spontaneous decompositions agrees well with that of a reaction of the first order. Therefore, from the above results, isotherms may be constructed showing the partial course of the inactivating reaction here concerned, at different temperatures. It is thus possible to find the time required to inactivate a given amount of thermolabile substance at the various temperatures. The reciprocals of the time may now be substituted in the above equation of Arrhenius, and the value of μ determined.

When these steps are followed, the inactivating reaction shows a constant value of $\mu = 66{,}800$. High values for μ, of the same order of magnitude as here given, obtain generally for spontaneous destructions, inactivations, and coagulations. The fact that the value of μ corresponds to those found for similar processes strengthens the force of the reasoning which underlies the analysis here presented.

It is, therefore, permissible to conclude that the duration of the latent period in the photic response of *Mya*, at the temperatures studied, is conditioned by two chemical reactions. The first is the fundamental reaction which determines the nature of the latent period. The second is a reaction which inactivates the principal product of the fundamental reaction, thereby prolonging the latent period at higher temperatures.